geodiversitas

1999 • 21 (2)



Publications Scientifiques du Muséum, Paris

geodiversitas fait suite,
avec la même tomaison, au Bulletin du
Muséum national d'Histoire naturelle,
4e série, section C, Sciences de la Terre.

geodiversitas est un trimestriel publié par les Publications Scientifiques du Muséum, Paris
geodiversitas *is a quarterly published by Publications Scientifiques du Muséum, Paris*

Abonnement pour l'année 1999 (prix HT)
Annual subscription rates 1999 (excluding VAT)
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Bivalves du Trias tariquide de Los Pastores (Algésiras), Espagne. Leur signification

Suzanne FRENEIX
Laboratoire de Paléontologie, UMR 8569 du CNRS,
Muséum national d'Histoire naturelle,
8 rue de Buffon, F-75231 Paris cedex 05 (France)

Freneix S. 1999. — Bivalves du Trias tariquide de Los Pastores (Algésiras), Espagne. Leur signification. *Geodiversitas* (21) 2 : 137-146.

RÉSUMÉ

La dalle calcaro-dolomitique fossilifère, découverte dans le roc de Los Pastores, à l'ouest d'Algésiras contient deux lits, plus carbonatés, à faunule de bivalves. Ceux-ci se présentent en valves dissociées de moules internes à la surface supérieure de la dalle et de moules externes incomplets, non déterminables, à la surface inférieure. Sept espèces, en concordance avec les espèces trouvées dans d'autres localités d'Espagne, ont été identifiées : ? *Gervillia joleaudi*, *Leptochondria alberti*, ? *Posidonia obliqua*, *Costatoria* (*Costatoria*) *goldfussii*, *Lyriomyophoria sublaevis*, *Neoschizodus* (*N.*) *laevigatus*, *Pseudocorbula gregaria*. Après une révision taxinomique, la signification de cet assemblage est considérée : (1) selon la distribution stratigraphique de ces espèces, parmi les domaines triasiques germanique, alpin-téthysien et d'Espagne, l'âge suggéré est Ladien supérieur-Carnien inférieur ; (2) quelques données de corrélations ressortent du biofaciès précédent souvent cité dans le Trias des Catalanides et des cordillères bétiques du domaine « séphatade ». Cependant, le biofaciès à *Lyriomyophoria sublaevis* prédominante paraît caractéristique de ce gisement méridional d'Andalousie ; (3) cette thanatocénose reflète un paléoenvironnement marin, peu profond, de haute énergie.

MOTS CLÉS
Bivalves (mollusques), Trias, Tariquides, Algésiras, Espagne, taxinomie, paléobiogéographie, biostratigraphie, paléoécologie.

ABSTRACT
Bivalves from the Tariquide Trias of Los Pastores (Algesiras), Spain.
A fossiliferous limestone slab from the Triassic locality of the Roch of Los Pastores (Algesiras W), yielded two beds of a bivalve faunule. The bivalves are preserved as dissociated valves of internal moulds on the upper side of the slab and as unidentifiable external moulds on its lower side. Seven species, similar with taxa known from other localities in Spain have been identified: ?*Gervillia joleaudi*, *Leptochondria alberti*, ?*Posidonia obliqua*, *Costatoria* (*Costatoria*) *goldfussii*, *Lyriomyophoria sublaevis*, *Neoschizodus* (*N.*) *laevigatus*, *Pseudocorbula gregaria*. The significance of this assemblage is considered after a systematic study: (1) according to the stratigraphical distribution of these seven species, particularly among the Germanic, the Alpine-tethyan and the Spanish Triassic realms, the age suggested is upper Ladinian-lower Carnian; (2) some correlations appear with the association: ?*Gervillia joleaudi*, *Leptochondria alberti*, *Neoschizodus laevigatus*, *Myophoria goldfussii*, *Lyriomyophoria sublaevis*; this last species is known from several fossilerous localities in the Catalanid and Betic Ranges into the "Sephardic" realm. However, the studied bivalve assemblage, with the dominant species *Lyriomyophoria sublaevis*, shows a characteristic biofacies, endemic of this southern province of Andalusia; (3) the *Lyriomyophoria* biofacies, with its condition of preservation, signifies a high energy, shallow, marine paleo-environment.

KEY WORDS
Bivalves,
Triassic,
"Tariquides",
Algesiras,
Spain,
taxonomy,
paleobiogeography,
biostratigraphy,
paleoecology.

INTRODUCTION STRATIGRAPHIQUE ET STRUCTURALE

La dalle carbonatée ayant livré les bivalves, objet de ce travail, provient d'un niveau du Trias appartenant à une succession mésozoïque originale qui apparaît dans les rochets de Los Pastores, à la sortie ouest de la ville d'Algésiras. Cet affleurement d'un-demi kilomètre carré est traversé par la route N-340 vers Tarifa. Il s'intercale tectoniquement dans les flyschs crétacés-paléogènes du Campo de Gibraltar.

Los Pastores, le roc de Gibraltar et le Jebel Moussa (Rif marocain) sont situés de part et d'autre du Détroit de Gibraltar. Ils ont été rassemblés (Durand-Delga 1972) dans un même ensemble tectonique et paléogéographique, les « Tariquides ». D'appartenance structurale discutée, cet ensemble se situe près du contact majeur qui sépare les zones externes (flyschs allochtones) des zones internes (Dorsale calcaire), dans l'arc qui unit cordillères bétiques et Rif.

Le Trias de Los Pastores (Baudelot *et al.* 1993, figs 1, 2) comprend de bas en haut :
1. marnes et gypses clairs (plus de 80 m) ;
2. pélites colorées (20 m) ;
3. grès clairs (20 m) à stratifications obliques ;
4. pélites colorées (30 m) avec quelques intercalations de bancs de dolomies plus ou moins calcareuses ;
5. dolomies grises à passées pélitiques sombres (30 m), que surmontent de puissantes dolomies (Trias supérieur) et calcaires (Lias inférieur) dans le rocher de Gibraltar.

Des associations palynologiques ont été dégagées des termes 2 et 4 (Carnien inférieur) et du terme 5 (Carnien moyen). L'horizon grès carbonaté à bivalves couronne une barre (2 m) formée de bancs calcaro-dolomitiques amalgamés. Elle se place aux deux tiers supérieurs du terme 4, dans des pélites lie de vin et verdâtres. Le point fossilifère étudié est à environ 200 m au sud du carrefour entre la route N-340 et la voie du Poligono

Industrial. En 1988, avant que la zone ne soit recouverte de déblais des grandes carrières, au sud de la route, la barre à bivalves se suivait, plongeant à l'est en série normale, en conservant ses caractères.
L'étude paléontologique entreprise est la suite logique de la publication sur le Trias des « Tariquides » (Baudelot *et al.* 1993).

TAPHONOMIE DES BIVALVES

Une dalle calcaro-dolomitique fossilifère, mesurant 35 cm × 23 cm et 7 cm d'épaisseur, a été extraite de la formation triasique du gisement précédemment cité par M. Durand-Delga et M. Esteras au cours d'une mission géologique récente. Cette dalle présente, sur chacune de ses faces horizontales, un lit coquillier à mollusques bivalves. À la face supérieure, les coquilles incluses dans cette assise gisent à plat, la face convexe orientée vers le haut, en valves dissociées et en fragments au nombre de quatre-vingts environ. Cet assemblage, suppose-t-on, a été déposé par des courants à la surface du sédiment, les valves désunies trouvant une position d'équilibre sur leur face concave. À la surface inférieure de la dalle, les bivalves, plus rares, ne sont observables que par leur face interne dont il ne subsiste que le contour ou quelques fragments d'empreintes externes. Ces derniers ne sont pas déterminables. Par contre, sept espèces ont été identifiées (dont deux avec doute) dans l'horizon supérieur, en concordance morphologique externe avec celles publiées par les auteurs espagnols, car leur état de conservation, très incomplet, ne donne pas accès aux caractères internes.

SYSTÉMATIQUE PALÉONTOLOGIQUE

Pour le matériel examiné, l'étude systématique comprend une synonymie restreinte, la distribution stratigraphique et paléobiogéographique des espèces, plus particulièrement, leur distribution connue en Espagne.
Ce matériel est déposé au Laboratoire de Paléontologie du Muséum national d'Histoire naturelle de Paris (LPM, MNHN).

Classe BIVALVIA Linné, 1758
Sous-classe PTERIOMORPHIA Beurlen, 1944
Ordre PTERIOIDA Newell, 1965
Sous-ordre PTERIINA, Newell, 1965
Superfamille PTERIACEA Gray, 1847
Famille BAKEVELLIIDAE King, 1850
Genre *Gervillia* Defrance, 1820

? ***Gervillia joleaudi*** Schmidt, 1935
(Fig. 1A, B)

Gervillia sp. – Joleaud 1912 : 77, pl. 1.
Gervilleia joleaudi Schmidt, 1935 : 53, pl. 4, figs 17, 18, 20.
Gervillia joleaudi Schmidt – Lerman 1960 : 34, pl. 3, figs 14, 15 – Márquez-Aliaga, Hirsch & López-Garrido 1986 : 210, figs 4E, F. – Márquez-Aliaga & Montoya 1991 : pl. 2, fig. 3 (3).

MATÉRIEL. — Six spécimens de taille réduite (n° LPM-R. 62091), de 15 à 25 mm de diamètre antéro-postérieur, de 5 à 7 mm de diamètre umbono-ventral, certainement juvéniles.

DISTRIBUTION. — Trias moyen d'Algérie ; Anisien-Ladinien inférieur d'Israël. En Espagne : cordillère Ibérique, Ladinien moyen (Baléares), Ladinien supérieur d'Henarejos (faune de Cuenca), Chelve (faune de Valence) ; Ladinien supérieur-Carnien de la cordillère Bétique, Prébétique de Murcie (Cehegin), Subbétique de Jaén (Hornos Siles)...

REMARQUES
Leur assignation hypothétique est fondée sur la forme étroite légèrement incurvée ventralement, sur l'angle de 25° environ du bord dorsal et de l'axe d'allongement de la coquille et sur les stries commarginales distales en relief de la région postérieure et sur l'aile postérieure obtuse. *G. joleaudi « forma juvenis »* Schmidt (1935 : 56, pl. 4, fig. 19) du Langobardien d'Espejeras est peut-être proche de nos exemplaires, ses dimensions sont de 14 mm de longueur et de 4 mm de largeur.

Superfamille PECTINACEA Rafinesque, 1815
Famille AVICULOPECTINIDAE
Meek & Hyaden, 1865
Sous-famille AVICULOPECTININAE
Meek & Hayden, 1865
Genre *Leptochondria* Bittner, 1891

Leptochondria alberti (Goldfuss, 1836)
(Fig. 1C)

Monotis alberti Goldfuss, 1836 : 138, pl. 120, fig. 6a, b.
Pecten inaequistriatus Goldfuss – Wurm 1911 : 102, pl. 6, figs 8-10.
Velopecten albertii Goldfuss – Schmidt 1935 : 61, pl. 4, figs 30, 31.
Chlamys (*Velata*) *alberti* Goldfuss – Virgili 1958 : 464, pl. 8, fig. 2.
Pecten albertii Goldfuss – Lerman 1960 : 40, pl. 4, fig. 14.
Leptochondria alberti (Goldfuss) – Márquez-Aliaga, Hirsch & López Garrido 1986 : 212, fig. 4G (avec synonymie). – Márquez-Aliaga & Montoya 1991 : 118, pl. 2, fig. 3 (2b, 2c, 2d).

MATÉRIEL. — Un fragment d'une valve gauche (n° LPM-R. 62092) de 20 mm environ de hauteur, présentant des costules radiales de deux ordres ; celles du second ordre apparaissent par intercalation. Ce fragment se rapporte sans aucun doute à *L. alberti*, espèce très commune au Trias.

DISTRIBUTION. — Trias germanique (Buntsandstein à Lettenkohle) et Trias alpin (Scythien à Carnien). Anisien-Ladinien inférieur de Transjordanie, d'Israël. En Espagne : cordillère Ibérique, Ladinien d'Esporlas (Baléares), terme carbonaté supérieur du Muschelkalk, faune de Teruel (Royuela), de Cuenca (Henarejos) ; cordillère Bétique, Subbétique de Jaén.

Famille POSIDONIIDAE Frech, 1909
Genre *Posidonia* Bronn, 1828

? *Posidonia obliqua* Hauer, 1857
(Fig. 1D)

Posidonomya obliqua Hauer, 1857 : 152, pl. 2, fig. 9. – Philipp 1904 : 94, pl. 6, figs 23, 24. – Wurm 1913 : 574, pl. 19, fig. 6.
Posidonia oblicua Hauer – Virgili 1958 : 451, pl. 6, fig. 1.
Posidonia obliqua Hauer *in* Philipp – Ichikawa 1958 : 187, pl. 23, fig. 6.

MATÉRIEL. — Une valve gauche et trois valves incomplètes (n° LPM-R. 62093).

DISTRIBUTION. — Trias alpin (Ladinien des Alpes du Sud). En Espagne : Muschelkalk supérieur des Catalanides (Composines).

REMARQUES
La valve gauche ovalaire, de 20 mm de longueur et 13 mm de hauteur, d'indice des diamètres L/H = 1,5, se rapproche des dimensions données par Virgili avec L/H variant de 1,4 à 1,5, toutefois de taille plus petite. L'ornementation est composée de huit ou neuf cordons (ou lamelles) concentriques assez espacés, épais, irréguliers ; le bord postérieur est oblique, mais le spécimen a été déformé par compaction.

Sous-classe PALAEOHETERODONTA Newell, 1965
Ordre TRIGONIOIDA Dall, 1889
Sous-ordre TRIGONIINA Dall, 1889
Superfamille MYOPHORIACEA Bronn, 1849
Famille MYOPHORIIDAE Bronn, 1849
(ou Famille COSTATORIIDAE Newell & Boyd, 1975
= MINETRIGONIIDAE Kobayashi, 1954)
Genre *Costatoria* Waagen, 1906
Sous-genre *Costatoria* s.s.

Costatoria (*Costatoria*) *goldfussii*
(Alberti *in* Zieten, 1830)
(Fig. 1E)

Trigonia goldfussii Alberti *in* Zieten, 1830 : 94, pl. 71, fig. 1.
Myophoria kiliani Schmidt 1935 : 79, pl. 5, figs 31, 32.
Myophoria goldfussi (Zieten) – Virgili 1958 : 480, fig. 58 n° 9.
Costatoria (Costatoria) goldfussi (Alberti *in* Zieten) – Allasinaz 1966 : 690, pl. 50, figs 7-10.
Costatoria goldfussi (Alberti *in* Zieten) – Cox 1969 : 473, fig. D 63, 3a. - Tamura 1972 : 69, pl. 1, figs 17-20. – Márquez-Aliaga, Hirsch & López Garrido 1986 : 216, fig. 4B, C. – Márquez-Aliaga & Montoya 1991 : 120, pl. 1, figs 2, 7, pl. 2, fig. 4. – Pérez López, Fernández, Solé de Porta & Márquez-Aliaga 1991 : 144, pl. 1, figs 2, 5, 7.

MATÉRIEL. — Une valve droite, une valve gauche et un fragment d'empreinte externe (n° LPM-R. 62094).

DISTRIBUTION. — Espèce eurasiatique (depuis l'Europe jusqu'en Asie). Muschelkalk-Keuper inférieur d'Allemagne ; Ladinien-Carnien des Alpes du Sud. En Espagne, Ladinien supérieur-Carnien inférieur de la cordillère Ibérique : provinces de Teruel, Cuenca et Valence, branche Castellane (diverses formations dont celle de Royuela), cordillère côtière catalane.

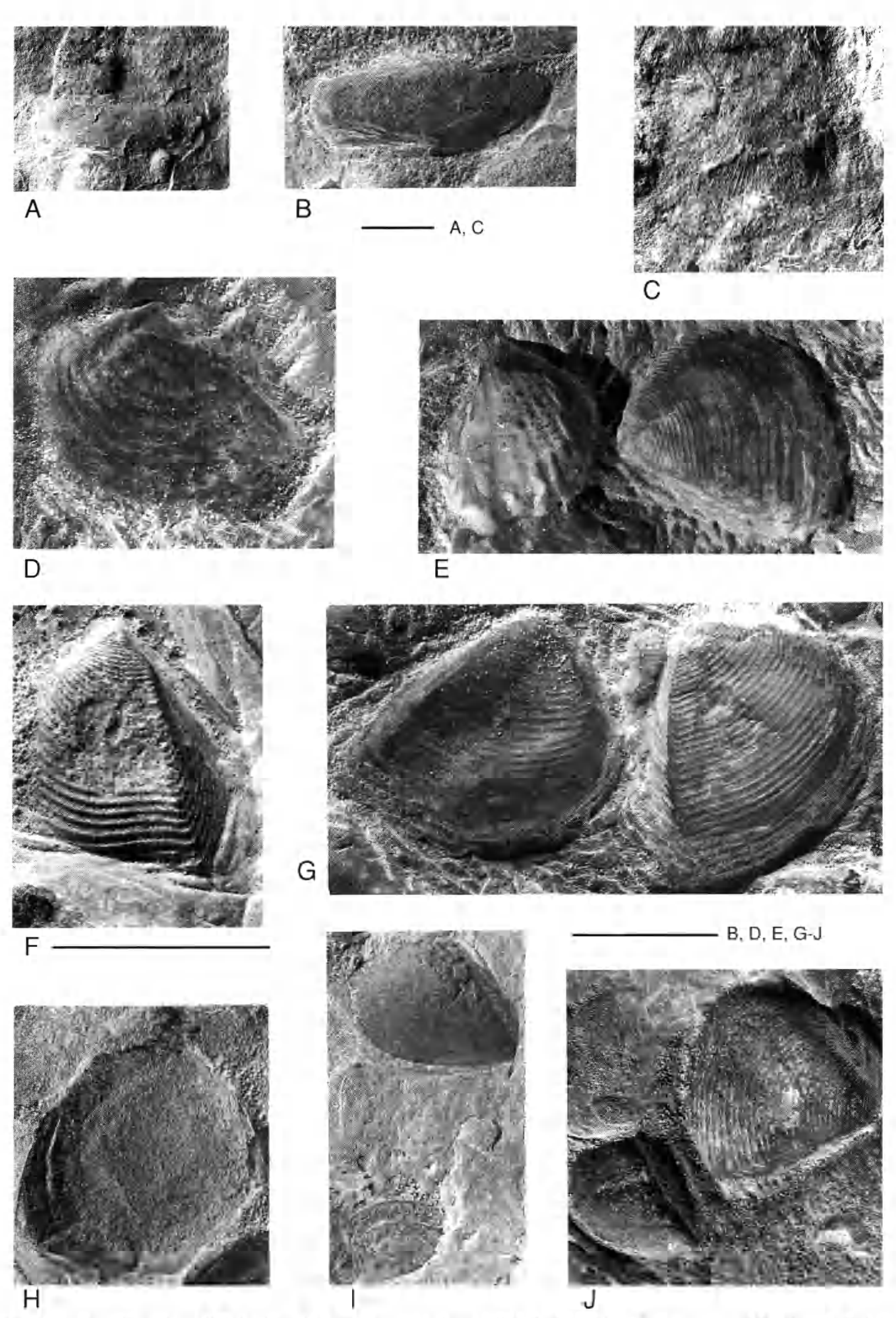


FIG. 1. — **A**, **B**, ? *Gervillia joleaudi* Schmidt, deux valves gauches (LPM-R. 62091) ; **C**, *Leptochondria alberti* (Goldfuss), valve gauche (LPM-R. 62092) ; **D**, ? *Posidonia obliqua* Hauer, valve gauche (LPM-R. 62093) ; **E**, *Costatoria* (*Costatoria*) *goldfussii* (Alberti *in* Zieten), valve droite (photo de gauche) et *Lyriomyophoria sublaevis* (Schmidt), valve droite (LPM-R. 62094) ; **F**, **G**, *Lyriomyophoria sublaevis* (Schmidt) ; **F**, valve gauche ; **G**, deux valves droites (LPM-R. 62095, LPM-R. 62096) ; **H**, *Neoschizodus* (*Neoschizodus*) *laevigatus* (Goldfuss), valve gauche (LPM-R. 62097) ; **I**, **J**, *Pseudocorbula gregaria* (Munster *in* Goldfuss) ; **I**, valve gauche, photographie du haut (LPM-R. 62098) ; **J**, autre valve gauche (photo du bas) avec *Lyriomyophoria sublaevis* (LPM-R. 620099). Clichés Denis Serrette (LPM, MNHN). Échelles : 1 cm.

Remarques

La valve droite la mieux conservée, de dimensions : H = 12 mm, L = 12 mm, est de forme trigono-ovale avec un crochet prosogyre, de position antérieure ; le flanc a dix à douze côtes radiales légèrement granuleuses que séparent des intervalles lisses plus larges que les côtes. Quelques côtes fines apparaissent près de l'umbo par intercalation. Des costules radiaires peu apparentes s'observent au bord de l'aréa mal conservée.

Genre *Lyriomyophoria* Kobayashi, 1954

Lyriomyophoria sublaevis (Schmidt, 1935) (Fig. 1E, F, K)

Myophoria sublaevis Schmidt, 1935 : 78, pl. 5, figs 27-30. – Virgili 1958 : 478, pl. 11, fig. 3.
Lyriomyophoria sublaevis (Schmidt) – Márquez-Aliaga & Montoya 1991 : 122, pl. 1, fig. 3. – Márquez-Aliaga & Martínez 1996 : 108.

Matériel. — Onze valves gauches, trois valves droites assez différentes des formes typiques décrites par Schmidt d'Espejeras (Alicante) et de Cehegin (Murcie) du Ladinien supérieur. Elles représentent un morphotype nouveau de rang infrasubspécifique.

Distribution. — Cette espèce est prédominante parmi la faunule étudiée de Los Pastores ; elle est fréquente dans les cordillères Ibérique et Bétique, particulièrement abondante dans le Ladinien supérieur-Carnien du Prébétique de Murcie, selon Márquez-Aliaga & Martínez (1996 : 108, 109).

Description

La forme trigone est d'une hauteur moyenne de 15 mm, d'une longueur moyenne de 16,5 pour un nombre de cinq spécimens, ayant les dimensions suivantes : H = 12 ; 14 ; 15 ; 17 et L = + 10 ; 16 ; 17 ; 20. La longueur peut être légèrement inférieure, égale ou un peu supérieure à la hauteur ; la moyenne de l'indice des paramètres L/H est proche de 114,8 %. Le galbe est peu convexe, les crochets sont situés aux deux cinquièmes environ antérieurs de la longueur ; l'angle umbonal oscille entre 85° et 100°. L'extrémité antérieure est ovalaire en continuité avec le bord ventral, tandis que le bord postérieur est légèrement convexe. La carène marginale est assez saillante (Fig. 1F) précédée d'une dépression antécarénale ; l'aréa est étroite, subdivisée par un sillon médian ; l'écusson est inobservable. Le flanc porte trente à trente-cinq côtes commarginales, régulières, denses dont les intervalles s'élargissent avec la croissance. Sur des hauteurs successives par intervalles de 3 mm, à partir du stade observable le plus juvénile, le nombre de costules concentriques descend de douze à neuf, à six, puis à cinq tout en s'épaississant et s'incurvant au niveau du sillon antécarénal et sur la carène marginale, avant de se poursuivre sur l'aréa. Cette costulation est plus dense, plus fine que celle connue par les illustrations des syntypes de Schmidt ou de celles d'autres auteurs (Virgili 1958 ; Márquez-Aliaga & Montoya 1991), soit dans le Muschelkalk supérieur de la cordillère côtière catalane, soit dans le Ladinien supérieur-Carnien des cordillères bétiques (zones externes : Prébétique et Subbétique).

Les différences entre les spécimens de Los Pastores et ceux d'autres localités, relatives à la taille plus petite, l'indice des dimensions L/H inférieur, les lignes de costules de croissance plus fines et régulières, n'autorisent pas leur attribution à un nouveau statut subspécifique pour ces variants. Ce sont des morphotypes ou morphes (Simpson 1961 : 178), soit des formes parmi un extrait de population fossile de faible effectif, donc de rang infrasubspécifique.

Genre *Neoschizodus* Giebel, 1855
Sous-genre *Neoschizodus* s.s.

Neoschizodus* (*Neoschizodus*) *laevigatus (Goldfuss, 1837) (Fig. 1H)

Lyrodon laevigatum Goldfuss, 1837 : 197, pl. 135, fig. 12 a, b.
Myophoria laevigata Alberti – Defretin, Durand-Delga & Lambert 1943 : 191, pl. 1, figs 10-12.
Myophoria laevigata Ziethen – Virgili 1958 : 476, pl. 11, fig. 9.
Neoschizodus laevigatus (Goldfuss) – Cox 1969 : 475, figs D 62, 7 a, b. – Newell & Boyd 1975 : 74, pl. 12, figs C, D 141, figs 82 A-D. – Tamura 1981 : 12, figs 12-18. – Marquez-Aliaga & Montoya 1991 : 121, pl. 1, fig. 1.

Neoschizodus laevigatus (Alberti) – Farsan 1972 : 178, pl. 45, fig. 7-3.
Neoschizodus (*Neoschizodus*) *laevigatus* (Goldfuss) – Fleming 1987 : 18, fig. 7 a, b.

MATÉRIEL. — Deux valves droites, une valve gauche (n° LPM-R. 62097), moules internes de forme ovale-arrondie de diamètres voisins de 22 mm, à carène postérieure peu marquée et d'aspect lisse, n'ayant conservé que quelques lignes de croissance commarginales.

DISTRIBUTION. — Eurasiatique : Buntsandstein supérieur à Lettenkohle d'Allemagne ; Werfénien à Ladinien des Alpes du Sud ; Anisien-Ladinien de Transjordanie et d'Israël ; Keuper d'Algérie ; Anisien-Norien d'Asie. En Espagne, de nombreux gisements de l'Anisien, Ladinien moyen et supérieur des cordillères *in* Márquez-Aliaga & Martïnez 1996 : 105, Ibérique, 107, Pyrénées catalanes ; 109, Bétique orientale (Prébétique et Subbétique)...

Sous-classe HETERODONTA Neumayr, 1884
Ordre VENEROIDA
H. Adams & A. Adams, 1856
Superfamille CRASSATELLACEA Férussac, 1822
Famille MYOPHORICARDIIDAE
Chavan & Cox [*in* Moore ed.], 1969
Genre *Pseudocorbula* Philippi, 1898

Pseudocorbula gregaria
(Münster *in* Goldfuss, 1837)
(Fig. 1I, J)

Nucula gregaria Münster *in* Goldfuss, 1837 : 152, pl. 124, fig. 12 a, b.
Myophoriopsis gregaria (Münster) – Schmidt 1935 : 84, pl. 5, fig. 36.
Pseudocorbula gregaria (Münster) – Farsan 1975 : 132, pl. 2, figs 9-12.
Pseudocorbula gregaria (Münster *in* Goldfuss) – Cox & Chavan 1969 : N 582, fig. 81, fig. 3a-d. – Márquez-Aliaga, Hirsch & López-Garrido 1986 : 18, fig. 4C (avec synonymie).

MATÉRIEL. — Deux valves gauches de hauteur de 7,5 et 9 mm pour une longueur de 12 et 10 mm (n° LPM-R. 62098).

DISTRIBUTION. — *Pseudocorbula gregaria* est à large répartition eurasiatique ; du Muschelkalk moyen et supérieur à la Lettenkohle d'Allemagne, Anisien des Alpes du Sud, Ladinien d'Afghanistan central. En Espagne : Ladinien-Carnien des cordillères Ibériques (terme carbonaté supérieur du Muschelkalk (provinces de Teruel, Cuenca, Valence) ; Ladinien supérieur de la branche Aragonèse ; Anisien-Ladinien des Catalanides ; Ladinien de la cordillère Bétique (Subbétique de Jaén, de Cadiz-Algésiras-Boyar) ; Ladinien-Carnien des Baléares.

REMARQUES
Leur forme est subtrigone, à carène postérieure peu élevée, délimitant une aire postérieure étroite limitée par un bord postérieur rectiligne oblique, puis droit à son extrémité distale. Ces individus se superposent, d'une part à la figure-texte donnée par Virgili (1958, fig. 59-5) pour l'espèce *gregaria* et d'autre part à celle de *Myophoriopsis* (*Pseudocorbula*) *keuperina* (Quenstedt 1851 ; Virgili 1958, fig. 59-2), espèce mise en synonymie avec la précédente par Márquez-Aliaga *et al.* (1986).

SIGNIFICATION DE LA FAUNE DE BIVALVES ET CONCLUSIONS

À partir de l'assemblage de bivalves étudié, provenant du gisement même de Los Pastores de la série Tariquide, il est possible d'envisager sa signification d'ordres biostratigraphique, paléobiogéographique, paléoécologique.
1. La distribution de ces espèces citées dans les divers domaines germanique, alpin-téthysien et, plus particulièrement, dans celui de l'Espagne est portée sur la Tableau 1. Leur association suggère d'assigner un âge Ladinien supérieur-Carnien inférieur à cette faune du rocher de Los Pastores, sans exclure toutefois le Carnien seul d'après les corrélations biogéographiques avec le Trias d'Espagne.
2. Les analyses, entre autres, de Hirsch (1977) dans le domaine sépharade permettent de relever, en effet, certaines affinités avec : (a) le Trias catalan, en particulier le Carnien inférieur à *Costatoria goldfussii*, le Langobardien avec *Lyriomyphoria sublaevis* ; (b) la faune de Royuela, région de Teruel des chaînes ibériques, compte tenu des espèces signalées, *Gervillia joleaudi*, *Leptochondria alberti*, *Costatoria goldfussii*, *Lyriomyphoria sublaevis*, *Neoschizodus laevigatus*, dont l'âge se situerait à la limite du Ladinien supérieur et du Carnien inférieur ; (c) la même association spécifique précédente des cordillères

TABLEAU 1. — Distribution stratigraphique des espèces de bivalves citées du Trias germanique, du Trias alpin-téthysien, du Trias d'Espagne. Dessin Françoise Pilard (LPM, MNHN).

ESPÈCES	Muschelkalk			Keuper inf.
	Anisien	Ladinien inf.	Ladinien sup.	Carnien
Gervillia joleaudi	— —	— — ——	——	
Leptochondria alberti	— · — —	— · — — ——	— · — — ——	— · — —
Posidonia obliqua		— —	— — ——	
Costatoria goldfussii	— · — —	— · — —	— · — — ——	— · — — → ——
Lyriomyophoria sublaevis			——	——
Neoschizodus laevigatus	— · — — ——	— · — — ——	— · — — ——	— — →
Pseudocorbula gregaria	— — ——	— · — — ——	— · — — ——	— · →

Trias germanique : — · Trias Alpin-Téthys : — — Trias d'Espagne : ——

bétiques, zone interne, prébétique de Jaén, récoltée dans une assise carbonatée du Ladinien supérieur ; (d) le membre sommital de la formation de Fuente Aledo (Murcie) des cordillères bétiques, zone interne, livrant *Costatoria goldfussii* et *Gervillia* cf. *joleaudi*, qui serait datée du Ladinien supérieur ; (e) toutefois, malgré les affinités relevées avec ces divers domaines paléobiogéographiques, l'assemblage de bivalves étudié présente une particularité : la prédominance sur les autres espèces de *Lyriomyophoria sublaevis* définissant un biofaciès à *Lyriomyophoria* du groupe *L. elegans*, signalé dans plusieurs horizons triasiques de différentes cordillères (Martin-Algarra *et al.* 1993 ; Márquez-Aliaga *et al.* 1996).

3. Les caractères taphonomiques de l'assemblage indiqués précédemment dont, en particulier, la désarticulation des valves stabilisées, leur surface externe convexe tournée vers le haut de la couche, laissent supposer un certain hydrodynamisme du milieu. Comme aucune direction préférentielle d'orientation des valves n'est observable, on peut en déduire qu'il s'agit d'une simmigie allochtone. La morphologie fonctionnelle des espèces, la sédimentologie originelle de leur milieu de vie supposent des implications. Les modes de vie tous filtreurs suspensivores se répartissent en deux groupes : épifaunique et infaunique.

L'épifaune comprend les espèces : ? *Gervillia joleaudi*, *Leptochondria alberti*, ? *Posidonia obliqua*. Les trois genres représentés (*Gervillia*, *Leptochondria*, *Posidonia*) sont épibenthiques, pseudoplanctoniques, oscillants ou pendants, fixés par des fils de byssus à des algues ou autres supports flottants ou fixés (Kauffmann 1969). Les juvéniles devaient être facilement détachés de leur support par l'agitation des eaux.

L'endofaune est composée des quatre espèces libres, fouisseuses dans des sédiments meubles : *Costatoria goldfussii*, *Lyriomyophoria sublaevis*, *Neoschizodus laevigatus*, *Pseucorbula gregaria*. Les

Myophoriidae auxquelles s'ajoute le crassatellacé *Peudocorbula* souvent opportuniste (Márquez-Aliaga & Garcia-Gil 1991), sont des fouisseurs superficiels actifs, en position de vie à la limite sédiments-eau que leurs zones exhalante et inhalante dépassent parfois.

En tant qu'ancêtres supposés des Trigoniidae, ils avaient la capacité, comme *Lyriomyophoria* (Stanley 1977 : 896), de s'adapter aux sédiments instables et aux variations de salinité.

4. Conclusions : la faune de bivalves étudiée, bien que de faible diversité, a permis de la situer, au Trias, dans le Carnien du domaine sépharade. Elle se caractérise par un biofaciès à *Lyriomyophoria sublaevis*. Son gisement de Los Pastores évoque un paléoenvironnement marin d'étagement infra-littoral peu profond, en bordure d'un estran gréso-carbonaté, peut-être pérideltaïque, car soumis à des fluctuations d'hydrodynamisme (courants, vagues, marées), de salinité, de température, sous climat tropical.

Remerciements

Je remercie vivement M. le Professeur M. Durand-Delga pour m'avoir confié l'étude de cet intéressant matériel, pour avoir participé à la rédaction du texte stratigraphique introductif et déposé la dalle fossilifère (n° ET. 674), enregistrée sous le n° 1993-1, dans les collections du Laboratoire de Paléontologie du Muséum national d'Histoire naturelle de Paris (LPM, MNHN). J'exprime ma gratitude, pour leurs judicieuses critiques, aux rapporteurs : Mlle Annie Dhondt, M. Philippe Bouchet, M. Manuel Estéras, Mme Anne-Marie Ohler. Mes remerciements s'adressent aussi à M. Denis Serrette pour les très bonnes photographies, à Mme Françoise Pilard dessinatrice, pour les illustrations, à Mme Danielle Quintus pour la saisie de texte, sans oublier M. Hervé Barrat pour l'aide apportée au dégagement très difficile du contour des fossiles.

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Soumis pour publication le 10 mars 1998 ;
accepté le 26 octobre 1998.

Un paléoniscoïde (*Pisces*, *Actinopterygii*) de Buxières-les-Mines, témoin des affinités fauniques entre Massif central et Bohême au passage Carbonifère-Permien

C. POPLIN
Laboratoire de Paléontologie, UMR 8569 du CNRS, Muséum national d'Histoire naturelle,
8 rue de Buffon, F-75231 Paris cedex 05 (France)
cpoplin@mnhn.fr

Poplin C. 1999. — Un paléoniscoïde (*Pisces*, *Actinopterygii*) de Buxières-les-Mines, témoin des affinités fauniques entre Massif central et Bohême au passage Carbonifère-Permien. *Geodiversitas* 21 (2) : 147-155.

RÉSUMÉ

Description d'un paléoniscoïde, *Progyrolepis heyleri* n. sp., d'après neuf maxillaires et mandibules isolés sur des plaques de schiste provenant du Permien inférieur (Autunien) du bassin de l'Aumance (Massif central). Ces pièces, de six à neuf centimètres de long, portent deux rangées de dents marginales (petites externes, grandes internes) côniques à chapeau d'acrodine. La plaque postorbitaire du maxillaire est assez longue, basse et trapézoïdale. L'attribution générique de ce poisson se fonde sur la similitude de son ornementation, très caractéristique, avec celle de *P. speciosus* (Carbonifère supérieur de Bohême). Ceci est une nouvelle indication de ce qu'il n'existait pas de barrière biogéographique entre les bassins limniques du Massif central et de Bohême à la fin du Carbonifère et au début du Permien.

MOTS CLÉS
Actinopterygii, paléoniscoïde, Autunien, France, Massif central, Bohême.

ABSTRACT

*A paleoniscoid (*Pisces, Actinopterygii*) from Buxières-les-Mines, evidence of faunal relationships between Massif central and Bohemia at the turn over between Carboniferous and Permian.*

Description of a paleoniscoid, *Progyrolepis heyleri* n. sp., based on nine isolated maxillaries and mandibles on shale slabs from the Lower Permian (Autunian) of the Aumance basin (Massif central). These specimens, six to nine centimeters long, have two rows of marginal teeth (external small, internal large), conical with an acrodin cap. The postorbital plate of the maxillary is rather long, low and trapezoidal. The generic attribution of this fish is based on the similitude of its very characteristic ornamentation with that of *P. speciosus* (Upper Carboniferous, Bohemia). This is a new indication that there was no biogeographical barrier between the basins of the limnic faunas of Massif central and of Bohemia during the Upper Carboniferous and Lower Permian.

KEY WORDS
Actinopterygii, Paleoniscoid, Autunian, France, Massif central, Bohemia.

INTRODUCTION

Les actinoptérygiens du Permien inférieur du bassin houiller de Buxières-les-Mines sont représentés le plus souvent par des os isolés. C'est pourquoi aucune détermination précise n'a pu être donnée jusqu'à présent dans les publications consacrées à la paléoichthyologie de ce bassin (Heyler 1984 ; Heyler & Poplin 1990). Le matériel décrit ici est également très partiel car il consiste en maxillaires et en mandibules isolés. Mais leurs caractéristiques permettent de mieux cerner leur appartenance taxinomique : il s'agit d'une espèce nouvelle attribuée au genre *Progyrolepis*. L'intérêt de cette étude ne se limite pas à la systématique, elle donne aussi quelques indications sur les relations paléobiogéographiques entre ce bassin et la Bohême aux confins du Carbonifère et du Permien.

PROVENANCES GÉOGRAPHIQUE ET STRATIGRAPHIQUE

Les spécimens ont été récoltés dans la dernière mine de Buxières (« Découverte n° III ») encore exploitée par les Houillères des bassins du Centre et du Midi dans le bassin de l'Aumance, qui fait partie des bassins carbonifères et permiens de l'Allier (Steyer & Escuillié 1997). Ils viennent de la Formation de Buxières datée du Permien inférieur et attribuée à l'Autunien en tant qu'unité lithostratigraphique (Steyer *et al.* en préparation).

HISTORIQUE

Les premières fouilles datent des années 1960-1970 par D. Heyler et par des géologues dont P. Debriette qui a découvert le maxillaire choisi comme holotype du nouveau taxon décrit ici. Heyler (1984 : 114) a mentionné cette pièce sans la décrire. Heyler & Poplin (1990) ont signalé la présence de pièces isolées évoquant *Progyrolepis speciosus* Fritsch, 1875 de Bohême. Depuis 1996, les activités sur le terrain ont repris grâce à la détermination des membres de l'association « Rhinopolis » : ce sont eux, dont J.-M. Pouillon, qui ont mis au jour les autres spécimens étudiés ici.

MATÉRIEL ET FOSSILISATION

Il s'agit de trois maxillaires et six mandibules isolés sur des plaques de schiste et visibles par leur face latérale ou par leur face mésiale. L'absence de traces de morsures écarte l'action de prédateurs et favorise plutôt l'idée d'une mort naturelle suivie d'une décomposition sur place. N'étant pas usés, ces éléments n'ont dû subir qu'un transport faible après leur désarticulation. Cette hypothèse est soutenue par le fait qu'un maxillaire droit et deux mandibules droite et gauche gisent à proximité les uns des autres sur une même plaque de schiste, suggérant qu'ils peuvent provenir du même individu.

SYSTÉMATIQUE PALÉONTOLOGIQUE

Classe OSTEICHTHYES Huxley, 1880
Sous-Classe ACTINOPTERYGII Woodward, 1891
Ordre PALAEONISCIFORMES Hay, 1929
Famille PYGOPTERIDAE Aldinger, 1937
Genre *Progyrolepis* Fritsch, 1895

Progyrolepis heyleri n. sp.

HOLOTYPE. — n° BUX 86, déposé dans les collections du Laboratoire de Paléontologie du Muséum national d'Histoire naturelle (Paris). Un maxillaire droit en vue latérale sans contrepartie. Figuré *in* Heyler 1997, fig. 9.

LOCALITÉ-TYPE. — Buxières-les-Mines (Allier, France), Découverte III.

ÂGE. — Permien inférieur.

ÉTYMOLOGIE. — Espèce dédiée à Daniel Heyler, premier paléontologue à avoir étudié l'ichthyofaune de Buxières-les-Mines.

AUTRE MATÉRIEL. — Collection personnelle de J.-M Pouillon : n° JMP 177, empreinte de la face latérale d'un maxillaire gauche et vue mésiale du bord dentaire sans contrepartie (figuré *in* Poplin 1997b, fig. 2) ; n° JMP 194 A et B, extrémité antérieure de mandibule gauche, partie et contrepartie. — Collection de l'association « Rhinopolis » à Buxières-les-Mines : n° BX 28089 B, grande plaque de schiste (60 cm × 46 cm) sans contrepartie, avec un maxillaire droit en vue mésiale, une mandibule droite en vue latérale (figurée *in* Poplin 1997b, fig. 1) et une mandibule gauche en vue mésiale ; BX 030895, une mandibule gauche en vue latérale sans contrepartie ; BX M 093 1/2 et 2/2, mandibule partie et contrepartie ; BX



FIG. 1. — *Progyrolepis heyleri* n. sp., Autunien de Buxières-les-Mines (Massif central, France) ; holotype, coll. MNHN, BUX 86 ; maxillaire droit, face latérale. Échelle : 1 cm.

260996 (6), fragment de mandibule gauche en vue latérale.
Il s'agit de collections privées.

DIAGNOSE. — *Progyrolepis* dont les maxillaires et les mandibules ont 6 à 9 cm de long, ce qui suppose une longueur totale de l'animal de 60 à 70 cm. Maxillaire : plaque postorbitaire trapézoïdale, assez longue et basse, plus haute postérieurement, avec une zone lisse le long de son bord antérieur et un angle postéro-inférieur marqué mais faible ; ornementation de fines rides et vermiculations et, le long du bord dentaire, de tubercules ; bord dentaire se relevant en courbe vers l'avant et formant un bourrelet visible sur la face latérale sur toute sa longueur. Mandibule : allongée, massive, relevée vers l'avant, sans processus coronoïde, ornée de rides irrégulières se résolvant en vermiculations le long des bords supérieur et inférieur. Dents marginales coniques pourvues d'un chapeau d'acrodine, à côtes verticales larges, disposées en une rangée latérale de dents nombreuses et petites et une rangée médiale de dents moins nombreuses, hautes (6 à 7 mm) à grande cavité pulpaire.

DESCRIPTION

Bien que les pièces soient isolées, la concordance de leurs caractères morphologiques, de leur taille et de la nature de leur ornementation indique sans conteste qu'elles appartiennent au même taxon.

Maxillaires (Figs 1-3)

La longueur des spécimens varie de 6,5 à 7,5 cm environ (ce qui résulte d'une variabilité individuelle et du fait que les extrémités des os ne sont pas toujours intactes). Ils comportent, comme chez les paléoniscoïdes, une partie sousorbitaire basse et une plaque postorbitaire haute. Celle-ci est trapézoïdale avec son bord supérieur plus court que l'inférieur et s'en écartant légèrement vers l'arrière de telle manière qu'elle atteint sa hauteur maximale au niveau de son quart postérieur (18 à 22,8 mm) ; son bord postérieur descend obliquement jusqu'à l'angle postéro-inférieur qui saille légèrement vers le bas. Le bord dentaire, légèrement sinusoïdal, se relève vers son extrémité antérieure. Les dents sont portées par l'habituel bourrelet longitudinal de la face interne, mais qui apparaît aussi sur la face externe en formant le long du bord inférieur un petit surplomb masquant un peu la base des dents. Le rapport de la longueur de la plaque postorbitaire sur sa hauteur est 2,1 en moyenne. Le rapport des longueurs de la plaque postorbitaire et du processus sousorbitaire est 2 en moyenne.

L'ornementation est complexe et originale. Sur la plaque postorbitaire, elle est constituée de nombreuses et fines rides irrégulières qui, *grosso modo*, sont parallèles aux bords supérieur et postérieur de l'os et forment parfois des boucles et de petits tourbillons (Fig. 3A). Vers le quart antérieur de la plaque, ces rides s'infléchissent vers le bas en dessinant une ligne verticale nette (Fig. 3B). En avant de celle-ci, quelques rides s'incurvent vers le bas et l'avant et se résolvent en petits tourbillons ; le reste de cet espace est lisse jusqu'au bord antérieur (Fig. 3B). Sur le bourrelet dentaire l'ornementation, longitudinale à l'arrière, se fragmente en tourbillons puis en fines vermiculations à l'avant (Fig. 3C). À proximité des dents, ce sont de petits tubercules arrondis (Figs 3F, E) portant des stries rayonnantes à partir de l'apex, comme chez *P. speciosus* (Fritsch 1895, pl. 131, fig. 15). À fort grossissement les rides révèlent un relief « en duvet » comme chez *Moythomasia nitida* Gross, 1953 (Jessen 1968, fig. 3), avec une fine crête médiane de laquelle partent de courtes crêtes latérales et régulières (Fig. 3E).

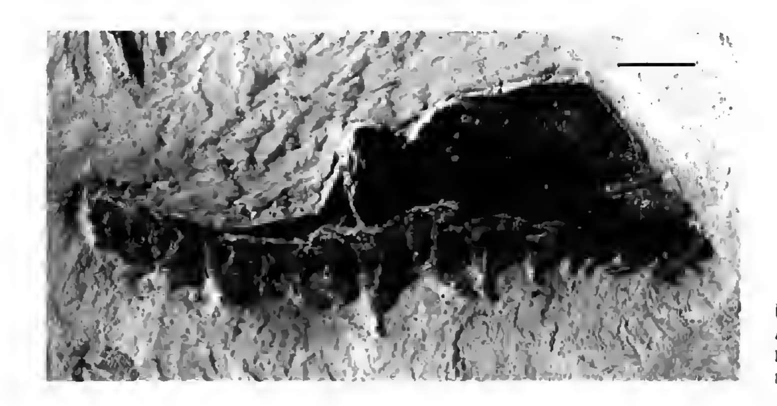


FIG. 2. — *Progyrolepis heyleri* n. sp., Autunien de Buxières-les-Mines (Massif central, France) ; coll. Rhinopolis BX 28089 ; maxillaire droit, face mésiale. Échelle : 1 cm.

Cetre ornementation varie d'un spécimen à l'autre dans le détail à l'insrar des dermaroglyphes. La zone lisse le long du bord antérieur de la plaque postorbitaire esr rare chez les paléoniscoïdes : on peut penser qu'elle était recouverte d'os sous- ou infraorbitaires du vivanr de l'animal.

Mandibules (Figs 4-6)
Les mandibules font 6 à 9 cm de long, donc un peu plus que les maxillaires : certe différence est courante chez les actinoptérygiens dont le maxillaire est précédé par les os du museau. Elles sont massives, allongées et sans processus coronoïde. Deux de ces pièces onr le bord dentaire courbé vers le haut er l'avant comme sur les maxillaires. Chez trois autres le bord dentaire semble rectiligne : s'agit-il d'une déformation post-mortem ?
La face latérale est constituée du dentalosplénial suivi de l'angulaire dont la suture est observée sur l'une des pièces. Sur la face mésiale le dentalosplénial apparaît ventralement avec, au dessus, l'os de Meckel. Le long du bord dentaire, une série de coronoïdes est suivie d'un large préarticulaire, mais les sutures ne sont pas nettes. Les deux facettes articulaires, à l'extrémité postérieure de l'os de Meckel, sont très apparenres sur les faces latérale et mésiale.
La fine ornementation consiste en rides longitudinales et en vermiculations le long des bords supérieur et inférieur.

Dents (Figs 1, 2, 4-6)
Les dents marginales sont côniques, portent un chapeau d'acrodine et sont lisses avec quelques côtes verticales larges. Elles sont disposées en deux rangées longitudinales : rangée externe de nombreuses petites dents (hauteur moyenne 1,9 mm au maxillaire et 1,6 mm à la mandibule), et rangée interne d'une dizaine de grandes dents (hauteur moyenne 7 mm au maxillaire et 6 mm à la mandibule) dont la base est un peu élargie par une vaste cavité pulpaire, visible sur plusieurs dents cassées. Sur le maxillaire n° Rhino Bx.28089B (Fig. 2) les alvéoles des dents internes sont contigus, mais il n'y a de dent en place que dans une alvéole sur deux : cette disposition doit être liée au remplacement dentaire car les grandes dents sont semblablement espacées sur les autres pièces.
L'angulaire et les coronoïdes sont couverts de dents minuscules (Figs 5, 6).

DISCUSSION

La présence du chapeau d'acrodine est particulière aux actinoptérygiens à l'exception de *Cheirolepis* Agassiz, 1835 (Patterson 1982 ; Arratia & Cloutier 1996). La plaque postorbitaire haute et longue du maxillaire ne s'observe que chez les Actinopteri basaux (Gardiner & Schaeffer 1989) nommés de manière informelle « paléoniscoïdes » ou « actinoptérygiens primitifs fossiles ». En effet, cette plaque fait partie d'un ensemble de traits morpho-foncrionnels liés au suspensorium des mâchoires : bouche et joue longues, hyomandibulaire er préopercule très inclinés. Il en est de même pour l'absence de processus coronoïde à la mandibule : celui-ci, très rarement observé chez les paléoniscoïdes (Poplin & Véran 1996), est caractéristique des néoptérygiens (Gardiner 1984). Enfin la disposition des dents marginales, grandes médiales er petires latérales, semble être primitive chez les actinopté-

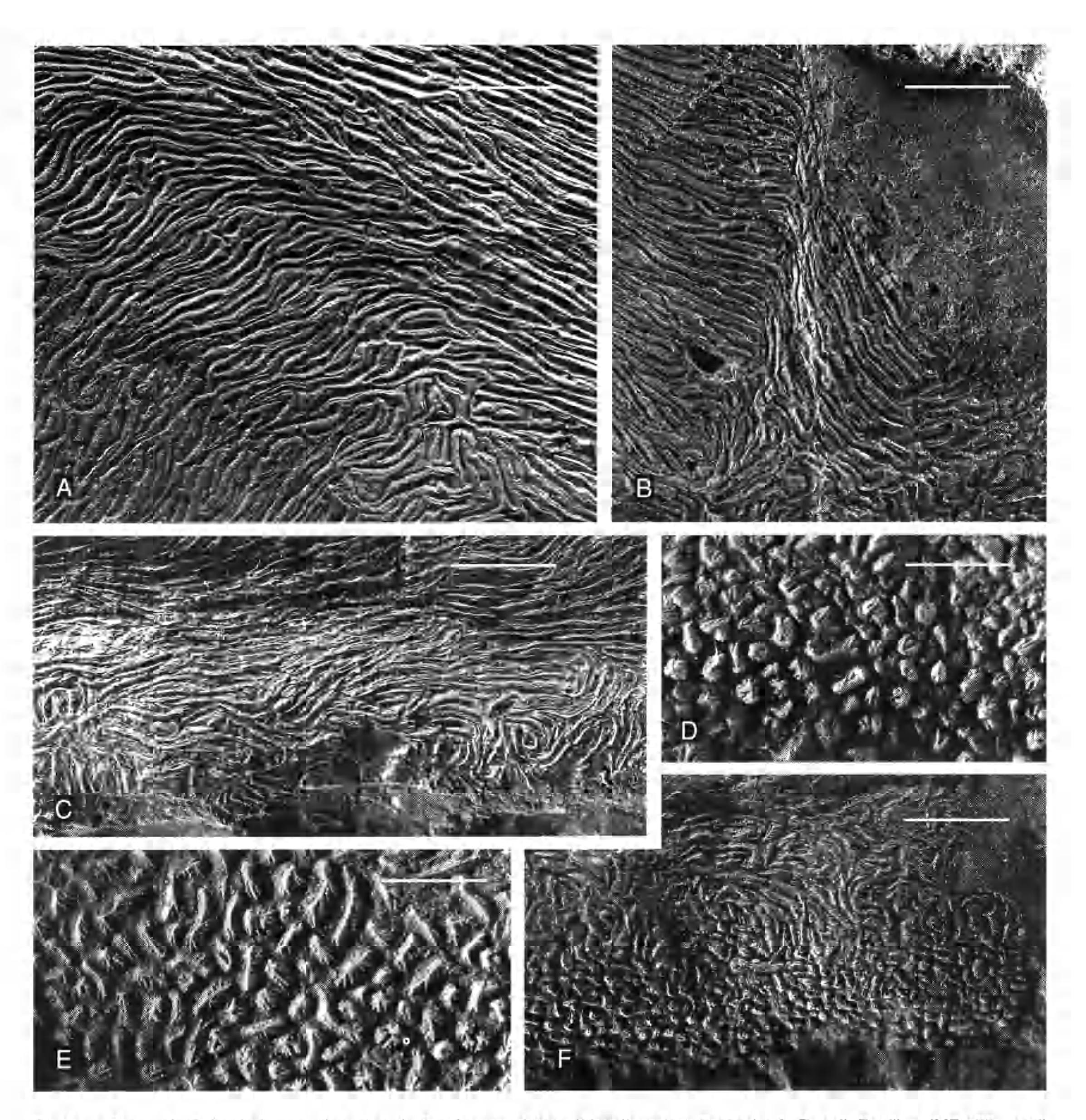


FIG. 3. — *Progyrolepis heyleri* n. sp., Autunien de Buxières-les-Mines (Massif central, France) ; **A**, **B**, coll. Pouillon JMP 177, maxillaire gauche, détails de l'empreinte de l'ornementation sur la plaque postorbitaire ; **A**, centre de la plaque ; **B**, ligne verticale antérieure ; **C**-**F**, holotype, coll. MNHN, BUX 86, maxillaire droit, détails de l'ornementation ; **C**, partie postérieure du bourrelet dentaire ; **D**, tubercules ; **E**, rides et vermiculations ; **F**, partie antérieure du bourrelet dentaire. Échelles : A-C, F, 2 mm ; D, E, 1 mm.

rygiens (Poplin & Heyler 1993). Il résulte de ce qui précède que cette espèce de Buxières est un actinoptérygien paléoniscoïde.

Mais ses affinités au sein de ce groupe sont plus difficiles à établir. Force est de porter attention à des caractères souvent traités comme mineurs : détails de la silhouette du maxillaire et de son ornementation, hauteur comparée et état de surface des dents. Cette recherche n'est guère facile car les descriptions des paléoniscoïdes ne sont pas toujours poussées à ce point de détails. Mais par chance l'un de ceux-ci, l'ornementation, est suffi-

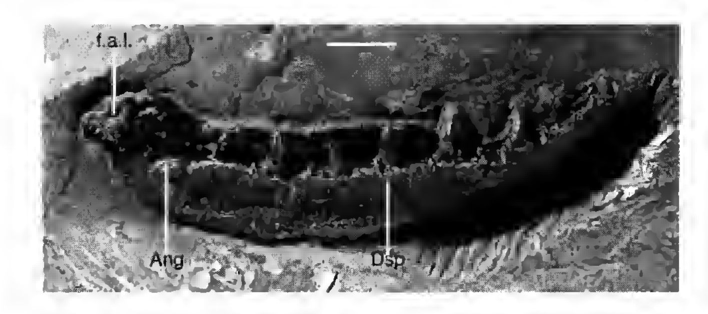


FIG. 4. — *Progyrolepis heyleri* n. sp., Autunien de Buxières-les-Mines (Massif central, France) ; coll. Rhinopolis BX 28089 ; mandibule droite, face latérale. **Ang**, angulaire ; **Dsp**, dentalosplénial ; **f.a.l.**, fossette articulaire latérale. Échelle 1 cm.

samment caractéristique et précis pour permettre l'attribution au genre *Progyrolepis*. La discussion ci-après est limitée aux trois genres directement concernés par cette nouvelle espèce.

1. Heyler (1977, 1997) a étudié une mandibule isolée du Permien de Lodève dont il a fait l'holotype du genre et de l'espèce *Usclasichthys macrodens* Heyler, 1977. Ce taxon est remarquable par la taille et la morphologie des dents marginales internes. Leur hauteur est plus grande que celle de la mandibule à leur niveau : ceci résulte du fait que leur moitié distale, qui a la forme cônique habituelle avec le chapeau d'acrodine, est portée par une base aussi haute et considérablement élargie en forme de coupole autour d'une cavité pulpaire très vaste. En outre, le bord dentaire porte de petites dents insérées en bouquet sur des capsules hémisphériques.

Heyler (1997) a fait une première description du maxillaire défini ici comme l'holotype de *Progyrolepis heyleri*. Remarquant sa taille, voisine de celle de l'espèce de Lodève, ainsi que la hauteur et la forme de ses grandes dents, il a émis l'hypothèse que ce maxillaire pouvait appartenir à une forme proche, voire à *Usclasichthys* même. Mais la base dentaire plus petite et l'absence de petites dents disposées en bouquets lui ont fait évoquer également la possibilité qu'il s'agisse d'un « actinoptérygien classique ». Cette dernière proposition est confirmée par l'observation précise des autres pièces (Poplin 1997b) : bien qu'élargie, la cavité pulpaire ne détermine pas de forme en coupole comme chez *Usclasichthys* Heyler, 1977 si bien que les dents sont moins hautes que la mandibule à leur niveau.

2. Nombre paléoniscoïdes ressemblent à l'espèce *Progyrolepis heyleri* par les grands traits de leurs mâchoires : plaque postorbitaire du maxillaire trapézoïdale et plus haute postérieurement, bouche incurvée vers le haut et l'avant, grandes dents marginales ayant une vaste cavité pulpaire, ornementation de rides de ganoïne. Parmi ces paléoniscoïdes, deux genres se distinguent par plusieurs caractères mineurs qu'ils partagent avec l'espèce de Buxières : *Nematoptychius* et *Progyrolepis*.

L'espèce type de *Nematoptychius* Traquair, 1875, *N. greenocki* Traquair, 1875, provient d'un milieu estuarien du Carbonifère inférieur d'Écosse. Ce poisson, long d'une quarantaine de centimètres, présente avec celui de Buxières les points communs suivants : le recouvrement de la plaque postérieure du maxillaire par les os postorbitaires et la surface des dents lisse à part quelques côtes larges sur la face linguale. Mais elle s'en distingue par l'angle postéro-inférieur du maxillaire très fort, la silhouette plus gracile de la mandibule et l'ornementation du maxillaire faite de simples rides régulières et de tubercules le long du bord dentaire (Traquair 1877, pl. I, figs 9, 11 ; pl. 26, figs 1, 5-7).

Progyrolepis speciosus (Fritsch, 1875), type du genre *Progyrolepis* créé par Fritsch (1895 : 118), vient du Carbonifère supérieur du bassin intramontagneux de Kounov (Bohême). Ce poisson est long de quelques 60 cm selon Stamberg (1991), comme, probablement, l'espèce de Buxières. Il partage avec cette dernière, outre la forme massive de sa mandibule, l'angle postéro-inférieur peu marqué du maxillaire et, surtout, l'ornementation des deux mâchoires (Fritsch 1895 : 119, pl. 131 fig. 12 ; Štamberg 1991 : 53, fig. 14, pls 5, 7, 9). En effet *P. speciosus* a exactement la même ornementation, dans son aspect et



FIG. 5. — *Progyrolepis heyleri* n. sp., Autunien de Buxières-les-Mines (Massif central, France) ; coll. Rhinopolis BX 28089 ; mandibule gauche face mésiale. **Cor**, coronoïdes ; **Dsp**, dentalosplénial ; **f.a.m.**, fossette articulaire médiale ; **mk**, os de Meckel ; **Par**, préarticulaire. Échelle : 1cm.

sa disposition, que les spécimens de Buxières. Il est inhabituel de fonder une attribution générique essentiellement sur l'aspect des reliefs de ganoïne des mâchoires ; mais cette ornementation est à ce point originale que le fait de la retrouver identique chez la forme de Bohême et celle de Buxières me pousse à en faire une synapomorphie de *Progyrolepis*. Le partage de ce caractère, ajouté aux autres cités plus haut, m'a décidée à attribuer le poisson de Buxières au genre *Progyrolepis*.

La création de l'espèce *heyleri* se justifie par les différences qu'elle présente avec l'espèce *P. speciosus* :

– la surface des dents. Chez *P. speciosus* (Fritsch 1895, pl. 132, figs 4-6) elle porte de nombreuses stries verticales entre lesquelles l'émail est couvert de minuscules tubercules ovoïdes réguliers : ce sont vraisemblablement des autapomorphies de *P. speciosus* ;

– l'absence sur le maxillaire de *P. speciosus* des caractères suivants de *P. heyleri* : ligne verticale d'ornementation de la plaque postorbitaire, et, en avant de cette ligne, surface lisse de recouvrement par les os sous- ou infraorbitaires, enfin bourrelet longitudinal du bord dentaire apparent sur la face externe ;

– les proportions un peu différentes de la plaque postorbitaire, plus longue chez *P. heyleri*. Chez *P. speciosus* le rapport de la longueur à la hauteur de la plaque postorbitaire est de 1,6 en moyenne ; celui des longueurs de la plaque postorbitaire et de la partie sousorbitaire est de 0,9 en moyenne (Stamberg 1991).

Ainsi le genre *Progyrolepis* comporterait actuellement deux espèces : *P. speciosus* (Fritsch, 1875) et *P. heyleri* (présent travail). Je suis pleinement d'accord avec Stamberg (1991) sur le fait que l'espèce *P. tricessimalaris* Dunkle, 1946 n'appartient pas à ce genre en raison de leurs différences ostéologiques, en particulier celles du maxillaire et du préopercule.

Avec un matériel limité aux maxillaires et mandibules, *P. heyleri* n'apporte pas d'arguments nouveaux sur les affinités de *Progyrolepis*, comme sur la suggestion de Fritsch (1895) selon lequel *Gyrolepis* Agassiz, 1833 serait intermédiaire entre *Progyrolepis* et *Acrolepis* Agassiz, 1833. Mais la comparaison faite plus haut entre *P. heyleri* et *Nematoptychius* Traquair, 1875 est significative : elle vient à l'appui du groupement de ces deux genres dans la famille des Pygopteridae (Stamberg 1991). Le cas de *Watsonichthys pectinatus* (Traquair, 1877) du Carbonifère inférieur d'Écosse va probablement dans le même sens. En effet, malgré des différences (plaque postorbitaire du maxillaire plus longue, mandibule moins massive, bords dentaires droits), il présente avec *Progyrolepis* une forte ressemblance concernant l'ornementation (Stamberg 1998).

CONCLUSION

Définir aux niveaux du genre et de l'espèce trois maxillaires et six mandibules isolés d'actinoptérygien paléoniscoïde était une gageure car ces pièces se distinguent par des caractères mineurs. Mais la chance a voulu que l'un de ceux-ci, l'ornementation, ait été déterminant en étant retrouvé à l'identique sur du matériel connu depuis plus d'un siècle et provenant d'une autre région et d'un autre étage stratigraphique. C'est ainsi que l'on peut résumer comment six pièces

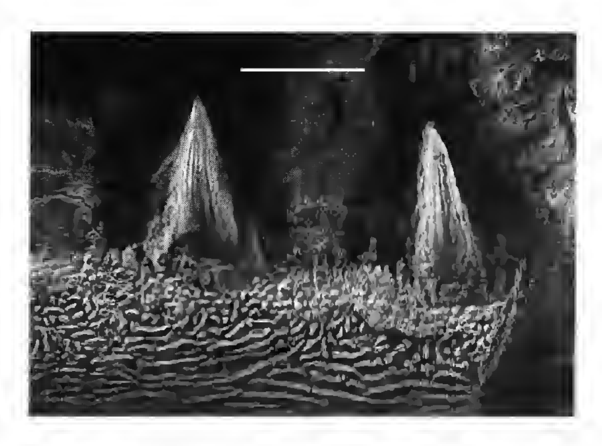


FIG. 6. — *Progyrolepis heyleri* n. sp., Autunien de Buxières-les-Mines (Massif central, France) ; coll. Rhinopolis BX 260996(6) ; détail de deux grandes dents marginales, vue latérale. Échelle : 4 mm.

isolées de l'Autunien de Buxières sont attribuées à *Progyrolepis heyleri* n. sp., dont le genre a été décrit pour la première fois dans le Carbonifère supérieur de Bohême par Fritsch en 1895. De cette histoire sont tirées une leçon et une conclusion.

La leçon est que, dans l'étude d'un matériel fossile, il ne faut négliger aucun spécimen : une pièce isolée peut donner des informations utiles. Il n'est pas mauvais de répéter cette vérité première à ceux, rares heureusement, qui ne consentent à travailler que sur les spécimens beaux et complets. Il n'en reste pas moins que la mise au jour à Buxières de tels spécimens en connexion de *Progyrolepis heyleri* est fortement souhaitée : ainsi pourront être précisée son anatomie et confirmées ses relations phylogéniques avec l'espèce de Bohême.

La conclusion est paléobiogéographique. *Progyrolepis* est une forme d'actinoptérygien présente à la fois à Buxières et en Bohême au tournant du Carbonifère et du Permien, comme *Paramblypterus* et des aeduelliformes (Stamberg 1985 ; Heyler & Poplin 1990). C'est là un nouveau témoin des fortes affinités fauniques maintes fois constatées à cette époque entre les bassins limniques du Nord du Massif central et ceux de Bohême (Poplin 1994, 1997a) et une démonstration de l'absence de barrière biogéographique entre ces deux territoires à la limite Carbonifère/Permien. Cette conclusion sera probablement un leitmotiv des travaux en cours sur les fossiles exhumés par les fouilleurs de l'association Rhinopolis à Buxières, en particulier les acanthodiens, les xénacanthiformes, les autres actinoptérygiens et les tétrapodes, sans oublier les invertébrés dont les insectes.

Remerciements

Je tiens à remercier l'association Rhinopolis et J.-M. Pouillon pour le prêt des spécimens étudiés ici, D. Heyler, H. Lelièvre et S. Stamberg pour de fructueuses discussions, H. Lavina pour la réalisation de la planche et D. Serrette pour celle des photographies.

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Soumis pour publication le 2 juin 1998 ;
accepté le 5 février 1999.

Restes de *Rhabdodon* (dinosaure ornithopode) de Transylvanie donnés par Nopcsa au Muséum national d'Histoire naturelle de Paris

Xabier PEREDA SUBERBIOLA
Universidad del País Vasco/Euskal Herriko Unibertsitatea,
Facultad de Ciencias, Laboratorio de Paleontología,
Apartado 644, E-48080 Bilbao (España)
gpbmubej@lg.ehu.es
Laboratoire de Paléontologie, Muséum national d'Histoire naturelle,
8 rue de Buffon, F-75231 Paris cedex 05 (France)

Philippe TAQUET
Laboratoire de Paléontologie, Muséum national d'Histoire naturelle,
8 rue de Buffon, F-75231 Paris cedex 05 (France)
taquet@mnhn.fr

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MOTS CLÉS
Dinosaure,
ornithopode,
Rhabdodon,
baron Nopcsa,
Crétacé supérieur,
Transylvanie.

RÉSUMÉ
Des restes de dinosaure provenant du Crétacé supérieur de Transylvanie ont été récemment retrouvés dans les collections du Muséum national d'Histoire naturelle de Paris. Il s'agit d'un dentaire, d'une scapula fragmentaire et de deux vertèbres caudales de l'ornithopode *Rhabdodon* (Iguanodontia). Cette collection fossile a été donnée au Muséum par le baron Nopcsa en 1923. Elle vient s'ajouter aux anciennes collections de reptiles fossiles provenant du bassin de Haţeg (Maastrichtien) qui sont déposées dans les musées de Londres et de Budapest.

KEY WORDS
Dinosaur,
ornithopod,
Rhabdodon,
Baron Nopcsa,
Late Cretaceous,
Transylvania.

ABSTRACT
Description of some Rhabdodon *remains (Dinosauria, Ornithopoda) from Transylvania, given by Nopcsa to the Museum national d'Histoire naturelle (Paris).*
Dinosaur remains from the Late Cretaceous of Transylvania have recently been found in the collections of the Muséum national d'Histoire naturelle of Paris. The material consists of a dentary, a fragmentary scapula and two caudal vertebrae from the ornithopod *Rhabdodon* (Iguanodontia). This collection is a present of Baron Nopcsa to the Muséum made in 1923. It adds to the old collections of fossil reptiles from the Haţeg Basin (Maastrichtian) kept at the museums of London and Budapest.

INTRODUCTION

Les premiers restes de dinosaures du Crétacé terminal du bassin de Haţeg (actuel comté de Hunedoara en Roumanie) ont été mis au jour en 1895. La découverte et l'étude des vertébrés fossiles de Transylvanie sont étroitement liées à la vie et à l'œuvre de Ferenc Nopcsa (Tasnádi-Kubacska 1945 ; Weishampel & Reif 1984 ; Pereda Suberbiola 1996). Le baron Nopcsa effectua de nombreuses prospections dans la région de Haţeg et entreprit des fouilles systématiques dans plusieurs gisements maastrichtiens (notamment Sânpetru et Vălioara). Il réussit à récolter une importante collection de reptiles fossiles, principalement des dinosaures, qu'il décrivit dans une série d'articles (Nopcsa 1900, 1902a, 1902b, 1904, 1914, 1915, 1923a, 1925, 1929). La collection de dinosaures réunie par Nopcsa, qui inclut des restes d'ornithopodes (*Telmatosaurus* Nopcsa, 1903 ; *Rhabdodon* Matheron, 1869), d'ankylosaures (*Struthiosaurus* Bunzel, 1870), de sauropodes titanosaures (*Magyarosaurus* Huene, 1932) et de théropodes, est l'une des plus importantes du Crétacé supérieur d'Europe (Weishampel *et al.* 1991).

Le but de ce travail est de décrire quelques ossements de dinosaure ornithopode provenant des sédiments finicrétacés de Transylvanie, récemment découverts dans les collections du Muséum national d'Histoire naturelle (MNHN) de Paris. Ces os font partie de l'assemblage dinosaurien récolté dans le bassin de Haţeg et ont été donnés par Nopcsa au MNHN de Paris. Cette description est l'occasion de faire un bilan du sort des anciennes collections de reptiles fossiles de Transylvanie.

PROVENANCE DU MATÉRIEL

Les os proviennent du Crétacé supérieur du bassin de Haţeg, comme l'indique une étiquette écrite en français et conservée dans la même boîte que les fossiles, où on peut lire : « Crétacé supérieur de Hongrie. Don de F. Nopcsa ». Le cahier d'entrées du Muséum national d'Histoire naturelle de Paris permet de savoir que ces pièces ont été données par Nopcsa le 21 janvier 1923 pour échange éventuel avec d'autres spécimens. Elles ont été numérotées par la suite, en 1944.

Nopcsa était déjà venu en visite à Paris le 21 janvier 1904 pour étudier les reptiles fossiles de France présents dans les collections du Muséum et le 20 et le 21 mars 1905 pour étudier des ossements de dinosaures de Madagascar. Lorsqu'il fit ce don et ces visites au Muséum, le professeur Marcellin Boule était titulaire de la chaire de Paléontologie et directeur du laboratoire.

Il convient de rappeler que la Transylvanie (Siebenbürgen) faisait partie de l'Empire austro-hongrois jusqu'en 1920, date à laquelle elle fut intégrée à la Roumanie par le traité de Trianon. Nopcsa étant d'origine hongroise, la faune de dinosaures du bassin de Haţeg est décrite dans ses travaux comme provenant du Crétacé supérieur de Hongrie (Nopcsa 1923a). Ce détail a suscité des quiproquos parmi certains auteurs modernes en ce qui concerne la géographie des sites. De même, les principaux gisements de la région, à savoir Sânpetru et Vălioara (en langue roumaine) sont décrits dans les articles de Nopcsa avec les noms hongrois de Szentpéterfalva et Valiora respectivement.

Les formations Sânpetru et Densus-Ciula, qui ont livré les restes de vertébrés dans le bassin de Haţeg, sont d'âge maastrichtien (Grigorescu 1983 ; Weishampel *et al.* 1991).

DESCRIPTION

Le matériel comprend quatre os, à savoir une branche mandibulaire droite incomplète, deux vertèbres caudales et une scapula gauche fragmentaire (Figs 1-3). Ces restes pourraient appartenir à un ou à plusieurs individus. Les fossiles sont de couleur marron rougeâtre et conservent par endroits une gangue argileuse de couleur verdâtre à grisâtre. L'ensemble est inventorié sous le numéro de collection MNHN 1944.2.

Dentaire (MNHN 1944.2.1) (Fig. 1A-C)

Il s'agit d'un dentaire droit de petite taille (longueur conservée égale à 130 mm). Il est assez gracile et élancé. Le spécimen est relativement bien conservé mais ne porte plus aucune dent en place. L'extrémité antérieure est peu effilée et

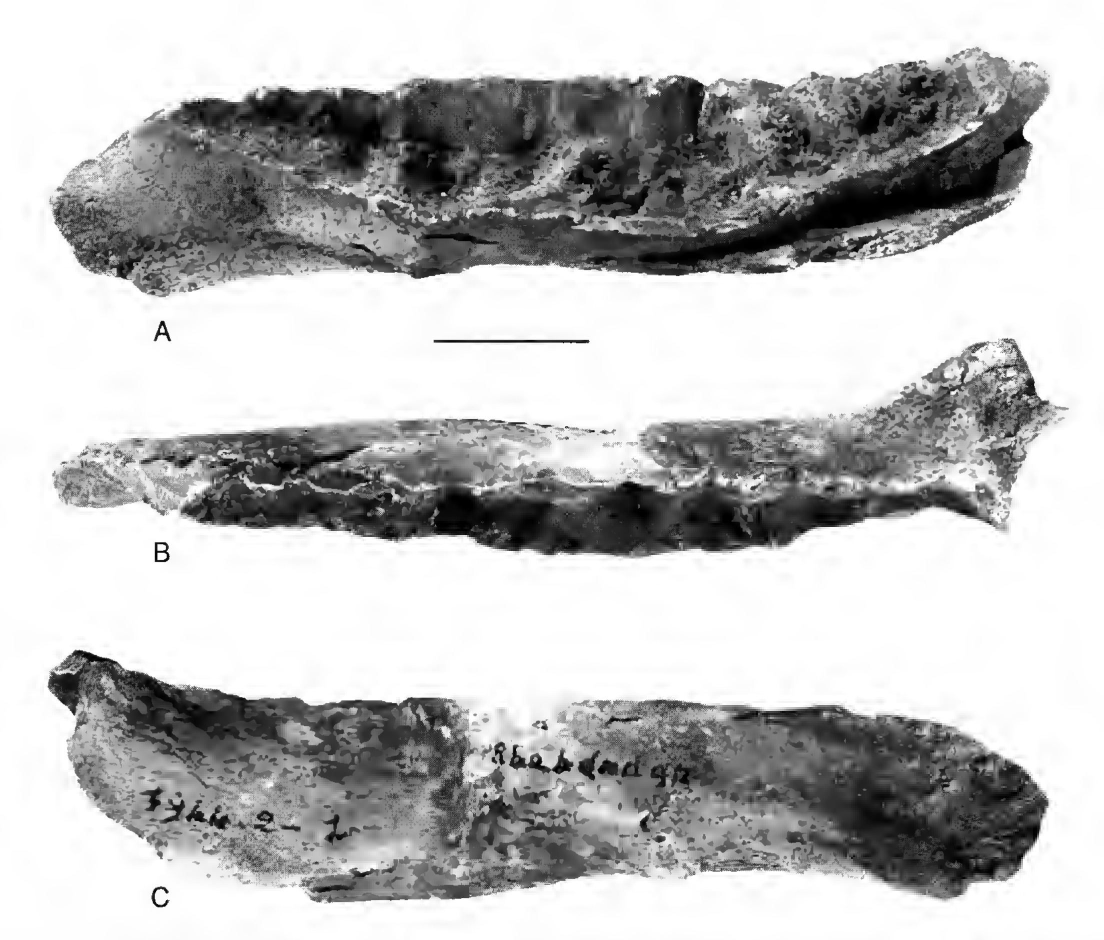
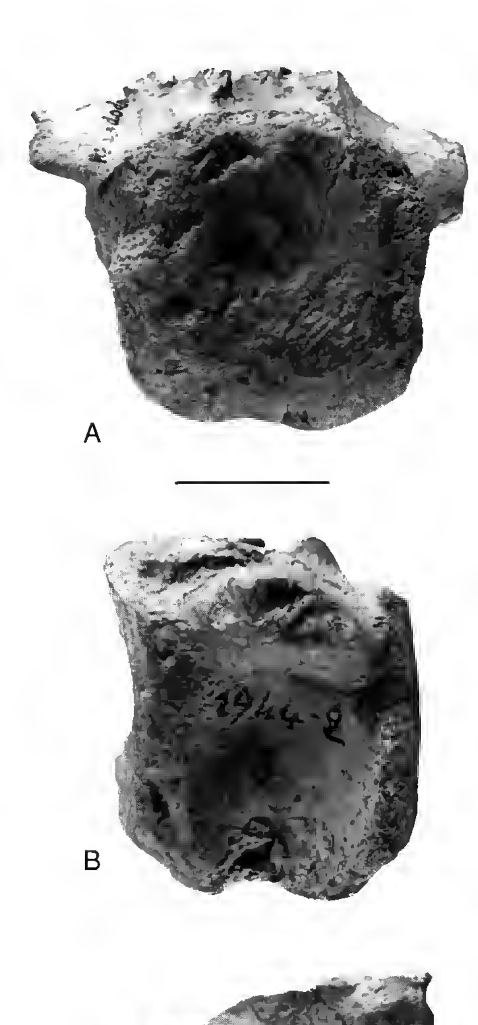


FIG. 1. — *Rhabdodon* sp., collection Nopcsa ; **A-C**, dentaire droit (MNHN 1944.2.1) ; **A**, vue médiale ; **B**, vue dorsale ; **C**, vue latérale. Échelle : 2 cm.

s'incurve ventromédialement pour former une courte symphyse mandibulaire. Les bords dorsal et ventral du dentaire sont à peu près parallèles. En vue latérale, le bord antérieur est rugueux et orné de plusieurs foramens nourriciers. Le prédentaire, absent, devait s'articuler avec le dentaire de telle sorte que son extrémité postérieure soit située à proximité du premier alvéole. Les parois latérale et médiale de la rangée alvéolaire, composée de dix alvéoles, ainsi que les parois interalvéolaires ont été partiellement reconstituées avec du plâtre peint en noir (une pratique jadis courante). La rangée alvéolaire est légèrement concave vers l'extérieur mais presque droite en vue occlusale. Les premier et dixième alvéoles sont les plus petits, tandis que les sixième et septième sont ceux qui ont la plus grande dimension. Le processus coronoïde est brisé et seule la partie basale est conservée. Ce processus est situé dans le prolongement de la rangée alvéolaire mais latéralement par rapport à celle-ci. Le splénial est absent, ce qui permet d'observer ventralement le canal de Meckel. Ce dernier forme un sillon étroit en avant qui devient plus large et profond vers l'arrière. Cette partie de la mandibule est aussi partiellement reconstituée. La face latérale du dentaire est très légèrement convexe vers l'extérieur et présente deux petits foramens nourriciers à la hauteur des alvéoles sept et huit. Ces foramens sont alignés en avant par rapport à un plateau latéral peu saillant situé au niveau du processus coronoïde.

Vertèbres caudales (MNHN 1944.2.3 et 4) (Fig. 2A-C)
Deux vertèbres sont connues, dont une provenant de la partie antérieure et l'autre de la partie médiane de la queue. La première comporte le centrum et l'extrémité proximale des processus transverses. Le centrum est platycoele à légèrement amphicoele, avec une surface articulaire antérieure circulaire et une postérieure ovoïde. La largeur du centrum (46 mm) est plus importante que la hauteur (42 mm) et que la longueur (environ 40 mm). Des facettes articulaires en forme de demi-lune destinées aux chevrons sont présentes sur la région ventrale. L'articulation avec les chevrons est intervertébrale. Les facettes postérieures sont plus développées que les antérieures. Elles délimitent ventralement un sillon profond de faible dimension. Les faces latérales du centrum sont concaves. Les processus transverses sont fragmentaires mais semblent disposés horizontalement.
La vertèbre caudale moyenne est relativement plus complète mais de plus petite taille. Elle reste partiellement recouverte par du sédiment. Le centrum et une partie de l'arc neural, y compris les postzygapophyses, sont conservés. L'épine neurale est brisée. La longueur du centrum (38 mm) est plus importante que la largeur (28 mm) ou que la hauteur (27 mm). Les surfaces articulaires sont circulaires à légèrement ovales. La surface ventrale présente un sillon longitudinal peu marqué, délimité en avant et en arrière par les facettes pour les arcs hémaux. Les postzygapophyses sont de petite taille et situées sur le bord postérolatéral de l'épine neurale. Elles ne dépassent guère le niveau de la face postérieure du centrum. Les processus transverses sont très peu développés et situés sur la moitié postérieure du centrum.



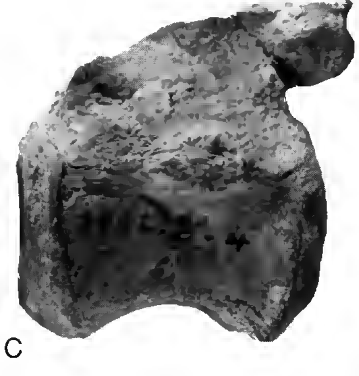


FIG. 2. — *Rhabdodon* sp., collection Nopcsa ; **A**, **B**, vertèbre caudale antérieure (MNHN 1944.2.3) ; **A**, vue postérieure ; **B**, vue latérale. **C**, vertèbre caudale moyenne, vue latérale (MNHN 1944.2.4). Échelle: 2 cm.

Scapula (MNHN 1944.2.2) (Fig. 3A-B)
Seul un fragment d'une scapula gauche est conservé. Le spécimen, long de 150 mm, comporte la région postéroventrale de l'extrémité proximale (y compris la cavité glénoïde et une partie de la surface pour le coracoïde) et le tiers proximal de la lame scapulaire. L'os présente une légère courbure à convexité latérale adaptée à la forme arrondie de la cage thoracique. La lame scapulaire, quoique fragmentaire, est mince (42 mm de largeur mesurée au niveau de la cassure) et semble s'élargir distalement. Le bord



Fig. 3. — *Rhabdodon* sp., collection Nopcsa ; **A**, **B**, scapula gauche (MNHN 1944.2.2) ; **A**, vue latérale ; **B**, vue postérieure. Échelle: 2 cm.

antérodorsal de la lame est droit, tandis que le bord postéroventral est concave. La surface latérale de l'extrémité proximale de la scapula présente une forte proéminence sur le bord postéroventral, en aplomb de la cavité glénoïde. En vue ventrale, la cavité glénoïde est une dépression plus longue que large, en forme de croissant. La surface pour le coracoïde est large et rugueuse.

DISCUSSION

La matériel décrit est rapporté aux Ornithopoda d'après sa morphologie générale. Les restes sont de dimensions plutôt modestes et appartiennent à un ornithopode de petite taille. L'arc neural et le centrum d'une des vertèbres caudales sont fusionnés : il ne s'agit donc pas d'un individu juvénile.

Le matériel de Hateg conservé à Paris peut être rapproché des Iguanodontia de part la combinaison de plusieurs caractères, à savoir : la présence d'un dentaire à bords dorsal et ventral parallèles, d'un processus coronoïde situé latéralement par rapport à la rangée dentaire, d'un diastème entre le prédentaire et le premier alvéole, d'alvéoles disposés sur le bord médial du dentaire, ainsi que la présence d'un contrefort saillant sur le bord postérieur de la cavité glénoïde sur la scapula (Sereno 1986 ; Norman & Weishampel 1990).

Le principal caractère diagnostique de *Rhabdodon* est la morphologie de ses dents et, plus spécialement, l'ornementation de l'émail dentaire (Brinkmann 1988 ; Weishampel *et al.* 1991). L'échantillon étudié ne comporte pas de dents mais, à défaut, la morphologie du dentaire est comparable à celle du matériel de *Rhabdodon* provenant de Transylvanie déposé à Londres (Nopcsa 1902a, 1925 ; Brinkmann 1988) et à Budapest (Nopcsa 1915). Le dentaire porte dix alvéoles et possède un petit diastème entre la surface pour le prédentaire et le premier alvéole, des caractères que l'on retrouve chez *Rhabdodon* (Weishampel *et al.* 1991). Il est à noter que, parmi les Iguanodontia, *Rhabdodon* présente le plus petit nombre connu de dents mandibulaires, De plus, la scapula présente une forte proéminence en forme de crochet sur le bord postérieur, comme c'est souvent le cas chez *Rhabdodon* (Brinkmann 1988). Le bord antérieur est droit comme chez certains spécimens de *Rhabdodon* provenant de Transylvanie (Brinkmann 1988) et chez *Tenontosaurus* (Forster 1990). D'autres scapulae de *Rhabdodon* peuvent montrer un bord antérieur concave, un caractère commun chez la plupart des Iguanodontia (Brinkmann 1988 ; Pincemaille 1997), Ces arguments nous amènent à rapporter le matériel étudié à *Rhabdodon*.

Les ornithopodes du bassin de Hateg incluent au moins deux genres, l'iguanodontien primitif *Rhabdodon* et l'hadrosauridé *Telmatosaurus* (Weishampel *et al.* 1991), *Rhabdodon* peut être distingué de *Telmatosaurus* par de nombreuses caractéristiques (Nopcsa 1900, 1902a, 1904, 1915, 1925 ; Brinkmann 1988 ; Weishampel *et al.* 1991), Le matériel conservé au MNHN de Paris peut être différencié de *Telmatosaurus* par le fait que la mandibule ne montre qu'une ébauche de batterie dentaire (bien développée chez tous les hadrosaures) et que les facettes pour l'articulation des chevrons sont fusionnées (divisées chez les hadrosaures).

Rhabdodon est par ailleurs le dinosaure le plus abondant du Crétacé supérieur de Transylvanie et d'Europe en général. Depuis Matheron, qui créa le genre en 1869 à partir de matériel trouvé dans le Rognacien (Maastrichtien) de Provence, de nombreux restes provenant du Campanien et du Maastrichtien de plusieurs contrées européennes lui ont été rapportés (voir Brinkmann 1988 pour un inventaire). *Rhabdodon* présente un forte variation individuelle, dont la signification n'est pas encore bien appréhendée (Pereda Suberbiola & Sanz 1999). Nopcsa (1915) évoqua un dimorphisme sexuel pour expliquer les différences morphologiques observées sur du matériel transylvain. Néanmoins, certaines d'entre elles peuvent être interprétées comme des différences ontogénétiques (Brinkmann 1988), Ce dernier auteur a proposé de rapporter tout le matériel de *Rhabdodon* à une seule espèce, *R. priscus* Matheron, 1869. Néanmoins, d'autres auteurs estiment que la diversité spécifique de *Rhabdodon* est plus grande que celle envisagée auparavant et plaident en faveur de la présence de plusieurs espèces (Buffetaut & Le Loeuff 1991). Le matériel provenant de Transylvanie a ainsi été rapporté à l'espèce *R. robustus* Nopcsa, 1900 (Pincemaille 1997 ; Weishampel *et al.* en préparation). L'échantillon conservé à Paris semble trop fragmentaire pour pouvoir tester cette interprétation. Il est donc rapporté à *Rhabdodon* sp. indet.

Enfin, la position phylogénétique de *Rhabdodon* au sein des ornithopodes est discutée. Il a d'abord été classé parmi les Camptosauridae (Nopcsa 1902a, 1904), puis rapproché des Iguanodontidae (Romer 1956), des Dryosauridae (Milner & Norman 1984) ou des Hypsilophodontidae (Norman 1984 ; Brinkmann 1988), avant d'être considéré comme un Iguanodontia primitif (Sereno 1986). Norman & Weishampel (1990), puis Weishampel *et al.* (1991) le classent provisoirement comme un Iguanodontia *incertae sedis*. Norman (1998) a défendu l'hypothèse selon laquelle *Rhabdodon* pourrait être un hypsilophodontidé qui montrerait des caractères conver-

gents avec les Iguanodontia, tout comme *Tenontosaurus* d'Amérique du Nord et *Muttaburrasaurus* d'Australie. Des analyses cladistiques récentes confirment l'hypothèse de Sereno (1986) et suggèrent que *Rhabdodon* se situe à la base des Iguanodontia dans une polytomie non résolue avec *Tenontosaurus*, *Mutaburrasaurus* et les Euiguanodontia de Coria & Salgado (1996) (Pincemaille 1997 ; Weishampel *et al.* 1998).

LES ANCIENNES COLLECTIONS DE DINOSAURES DE TRANSYLVANIE

Les anciennes collections de reptiles fossiles provenant du Crétacé terminal de Transylvanie sont conservées dans les musées de Londres et de Budapest. Une grande partie de la collection réunie par le baron Nopcsa et ses assistants dans les gisements du bassin de Haţeg fut vendue à plusieurs reprises au Natural History Museum de Londres (BMNH). La documentation officielle des Archives du BMNH atteste de l'achat de reptiles fossiles de la collection Nopcsa en 1906, 1923 et 1924 (S. Chapman, comm. pers.). Les deux premiers lots ont été vendus par Nopcsa lui-même et celui de 1924 eût comme intermédiaire le comte L. Szapáry, un ministre hongrois à Londres. La collection de 1906 inclut des spécimens provenant de Sânpetru, y compris les types des ornithopodes *Rhabdodon robustus* Nopcsa, 1900 et *Telmatosaurus transsylvanicus* Nopcsa, 1900 (Weishampel *et al.* 1991, 1993), ainsi que des restes de titanosaure[1]. Le matériel contient aussi des restes décrits à l'origine comme appartenant à des oiseaux (Andrews 1913), mais qui se sont révélés par la suite être de petits théropodes (voir un sommaire dans Weishampel & Jianu 1997). La collection de 1923, acquise pour 200 livres sterling, comprend des spécimens de Sânpetru et Vălioara, notamment les spécimens types de l'ankylosaure *Struthiosaurus transylvanicus* Nopcsa, 1929, du titanosaure *Magyarosaurus dacus* (Nopcsa, 1915) et de la tortue cryptodire *Kallokibotion bajazidi* Nopcsa, 1923 (Nopcsa 1923b, 1929 ; Huene 1932 ; Gaffney & Meylan 1992). Les archives du BMNH conservent des documents relatifs à cet achat, notamment une liste détaillée des ossements (environ deux cent soixante-cinq) et le prix approximatif de chaque échantillon. D'autres fossiles, comprenant des restes fragmentaires d'ornithopode, de titanosaure et de théropode, ont été donnés par Nopcsa au BMNH en 1909 et 1922. Une autre collection fut réunie par Lady Woodward à partir des gisements de Sânpetru et Nagy-Csula lors d'une visite dans les propriétés de la famille Nopcsa en Transylvanie. Celle-ci, qui contient en outre des restes de *Rhabdodon*, *Telmatosaurus*, *Magyarosaurus*, *Kallokibotion* et de petits théropodes, fut présentée au BMNH en 1923[2]. Le matériel conservé à Londres a été décrit par Nopcsa dans plusieurs articles, dont cinq dans la série dédiée aux dinosaures de Transylvanie (Nopcsa 1900, 1902a, 1904, 1925, 1929 ; voir aussi Nopcsa 1902b, 1923a). Il est intéressant de signaler qu'une collection de lames minces de reptiles fossiles, notamment de dinosaures, fut présentée par Nopcsa au BMNH en 1925. Certaines de ces lames ont été effectuées à partir du matériel dinosaurien de Transylvanie (Nopcsa & Heidsieck 1933).

Les collections de reptiles fossiles de Transylvanie conservées à Budapest au Magyar Állami Földtani Intézet (MAFI) incluent principalement des restes récoltés par le géologue Ottokar Kadić dans les environs de Vălioara pour le Ungarischen Geologischen Reichsanstalt. Les fouilles furent entreprises en 1914 (d'après les étiquettes du musée) ou 1915 (selon Kadić 1917). Les principaux spécimens ont été décrits par Nopcsa en 1915. Le matériel de dinosaure comprend des spécimens des ornithopodes *Rhabdodon robustus* et *Telmatosaurus transsylva-*

1. Nopcsa utilisa aussi les noms de *Limnosaurus* et d'*Orthomerus* pour se rapporter à *Telmatosaurus*, et celui de *Mochlodon* au lieu de *Rhabdodon* (Brinkmann 1988). Il attribua les restes de titanosaure au genre *Titanosaurus*, avant que von Huene ne propose le nom générique *Magyarosaurus* en 1932.

2. Il faut signaler à ce propos que Nopcsa entretint un lien très fort avec la famille Woodward, comme en témoigne la correspondance de 1906 à 1933 entre le baron et Sir Arthur Smith Woodward et le journal de Lady Woodward conservés aux archives du BMNH. A. S. Woodward était le responsable du département de Géologie du BMNH et pendant ses nombreux voyages à Londres, Nopcsa séjourna souvent chez les Woodward (S. Chapman, comm. pers.).

nicus, ainsi que du titanosaure *Magyarosaurus dacus*. Les autres reptiles représentés sont les crocodiliens (avec notamment le spécimen-type d'*Allodaposuchus precedens* Nopcsa, 1928) et les tortues. Les fonds du MAFI contiennent aussi des spécimens fossiles beaucoup plus fragmentaires d'une collection récoltée par Nopcsa luimême (L. Kordos, comm. pers.). Ils proviennent aussi de la localité de Văliora mais ne portent pas de date de collecte. En plus des restes d'ornithopode et de titanosaure, l'assemblage comprend un fragment de crâne d'un théropode Arctometatarsalia, récemment reconnu (Jianu & Weishampel 1997), des plaques de la carapace de *Kallokibotion* et des dents isolées de crocodile. Enfin, des restes de ptérosaure mis au jour par Nopcsa dans la région de Sânpetru (Nopcsa 1914) et longtemps considérés comme perdus, ont été retrouvés dernièrement dans les collections du MAFI (Jianu *et al.* 1997a). D'autres restes de dinosaure (*Telmatosaurus*) provenant de Sânpetru sont conservés au Magyar Nemzeti Múzeum (MNM) de Budapest (Weishampel *et al.* 1993). Ces pièces proviennent du MAFI et font probablement partie de la collection amassée par Kadić en 1914-1915 (D. Weishampel, comm. pers.).

La petite collection Nopcsa de dinosaure ornithopode du Muséum national d'Histoire naturelle de Paris vient s'ajouter à celles conservées à Londres et à Budapest. Dans une lettre adressée à son collègue et ami Friedrich von Huene, datée de 1924, Nopcsa mentionnait la présence dans le musée de Munich de quelques os de titanosaure provenant de Transylvanie (Tasnádi-Kubacska 1945). Ces os ont été soit récupérés par Nopcsa après cette date, soit détruits lors des bombardements de 1944 durant la Seconde Guerre mondiale. Toujours est-il qu'aujourd'hui, aucun reste de vertébré du bassin de Haţeg n'est déposé au musée de Munich (P. Wellnhofer, comm. pers.).

Il convient enfin de signaler que certains spécimens fossiles de la région de Haţeg ont été perdus. C'est le cas du matériel du dinosaure cuirassé *Onychosaurus hungaricus* décrit par Nopcsa en 1902 (Pereda Suberbiola & Galton 1997).

De nouvelles collections de vertébrés des gisements de Transylvanie ont été constituées plus récemment grâce aux efforts de plusieurs musées et institutions roumaines. C'est ainsi que les musées de Deva et les universités de Cluj-Napoca et Bucarest ont pu récolter de nouveaux restes de dinosaures (notamment des théropodes et des œufs d'hadrosaure), de crocodiles et de tortues, mais aussi des poissons osseux, des amphibiens et des mammifères multituberculés (Grigorescu 1983, 1984 ; Grigorescu *et al.* 1985, 1994 ; Weishampel *et al.* 1991 ; Jianu *et al.* 1997b). Un siècle après la première découverte de restes fossiles, le bassin de Haţeg est devenu une région fossilifère classique en Europe et une référence obligée pour les paléontologues qui s'intéressent aux faunes de vertébrés finicrétacés.

CONCLUSION

Une mandibule, deux vertèbres caudales et une scapula de dinosaure ornithopode provenant du Crétacé supérieur de Transylvanie font partie de la collection Nopcsa donnée par celui-ci au Muséum national d'Histoire naturelle en janvier 1923. Après étude, ces restes sont attribués à l'Iguanodontia *Rhabdodon*, notamment d'après la présence d'un dentaire à bords dorsal et ventral parallèles portant uniquement dix alvéoles, ainsi que d'une scapula à bord antérodorsal droit et montrant une forte proéminence sur le bord postéroventral. Ce matériel fournit des informations historiques complémentaires sur le sort des anciennes collections de dinosaures et autres reptiles fossiles de Transylvanie.

Remerciements

Nos remerciements à Mr. John Thackray (Archives, The Natural History Museum) pour avoir permis au premier auteur de consulter la correspondance du baron Nopcsa conservée à Londres, à Mrs. Sandra Chapman pour l'accès à la collection Nopcsa de reptiles fossiles conservée au BMNH, ainsi que pour ses renseignements sur le matériel fossile, aux Drs László Kordos (Magyar Állami Földtani Intézet, Budapest), Itsván Főzy (Természettudományi Múzeum, Budapest), M. Coralia Jianu (Muzeul Civilizatiei Dacice si Romane, Deva), Vlad Codrea

(Universitatea Babes-Bolyai, Cluj-Napoca), David B. Weishampel (The Johns Hopkins University, Baltimore) et Peter Wellnhofer (Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich) pour les données fournies sur les collections de vertébrés de Transylvanie, enfin, au Dr. David B. Norman (Sedgwick Museum, Cambridge) et à un rapporteur anonyme pour la relecture critique du manuscrit. Nous exprimons aussi toute notre gratitude à Mme Françoise Pilard pour son aide et à M. Denis Serrette pour les photographies des pièces.

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Soumis pour publication le 25 mars 1998 ;
accepté le 16 novembre 1998.

Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna, Cedar Mountain Formation, Utah, USA

Richard L. CIFELLI
Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma,
1335 Asp Ave., Norman, Oklahoma 73019 (USA)
rlc@ou.edu

Scott K. MADSEN
Dinosaur National Monument,
P. O. Box 128, Jensen, Utah, 84035 (USA)

Cifelli R. L. & Madsen S. K. 1999. — Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna, Cedar Mountain Formation, Utah, USA. *Geodiversitas* 21 (2) : 167-214.

ABSTRACT
Symmetrodont mammals, generally rare and poorly represented in the fossil record, are exceptionally abundant in the Mussentuchit local fauna of the upper Cedar Mountain Formation (upper Albian or lower Cenomanian), Emery County, Utah, USA. Herein we describe three new species of symmetrodonts (four or more are present in the fauna); one is referable to *Spalacotheridium*, otherwise known from the Turonian (Late Cretaceous), and the other two are referred to a new genus. With the possible exception of *Mictodon*, all North American Cretaceous symmetrodonts are referable to the Spalacotheriidae. Spalacotheriids are distinctly different from more primitive symmetrodonts such as *Kuehneotherium* in jaw structure (e.g., detachment of postdentary elements, presence of pterygoid crest) and molar morphology and function (e.g., development of continuous mesial and distal shearing surfaces). To this extent, they are more clearly similar to tribosphenic therians than are archaic symmetrodonts, although they are uniquely specialized. Some features of advanced spalacotheres, such as the loss of the coronoid and meckelian groove, developed convergently in tribosphenidans and many other groups, and hence represent iterative themes in the evolution of Mesozoic mammals. Features of the molars and dentary suggest that the Family Spalacotheriidae is a monophyletic group, with the European *Spalacotherium* and Chinese *Zhangheotherium* forming successive outgroups to remaining genera. Within the family, North American taxa appear to form a monophyletic clade, culminating in the highly specialized *Symmetrodontoides* of the Late Cretaceous; *Microderson*, known only by a single upper molar from the Cretaceous of Morocco, is of enigmatic affinities. Spalacotheriids were clearly present in North America by the Aptian-

KEY WORDS
Symmetrodonta,
Spalacotheriidae,
phylogeny,
Cretaceous.

Albian and, assuming that North American taxa form an endemic and exclusive monophyletic group, their presence on the continent cannot be attributed to an hypothesized mid-Cretaceous interchange with Asia. Instead, phylogenetic data suggest their origin from western Europe sometime in the Early Cretaceous, supporting the hypothesis that there was some degree of faunal continuity at that time between the two landmasses, based initially on similarities of the dinosaur assemblages.

RÉSUMÉ

Les symmétrodontes spalacotheriidés (Mammalia) du Crétacé (Albien supérieur ou Cénomanien inférieur) de la faune de Mussentuchit, Formation Cedar Mountain, Utah, USA.

Les mammifères symmétrodontes, qui sont généralement rares et mal représentés dans le registre fossile, sont exceptionellement abondants dans la faune locale de Mussentuchit du sommet de la Formation « Cedar Mountain » (Albien supérieur ou Cenomanien inférieur), Emery County, Utah, USA. Nous décrivons ici trois nouvelles espèces de symmétrodontes (il existe au moins quatre espèces dans la faune de Mussentuchit) ; une espèce se rapporte au genre *Spalacotheridium*, connu par ailleurs dans le Turonien (Crétacé supérieur), et les deux autres sont attribuées à un nouveau genre. À l'exception, peut-être, de *Mictodon*, tous les symmétrodontes nordaméricains appartiennent à la famille des Spalacotheriidae. Ces derniers diffèrent nettement des symmétrodontes plus primitifs tels que *Kuehneotherium* par la structure de leur mâchoires (entre autres, le détachement des éléments postdentaires et la présence d'une crête ptérygoïde) et par la morphologie et la fonction de leurs molaires (entre autres, le développement de surfaces coupantes continues mésiales et distales). Sur ce plan, ils ressemblent plus à des thériens tribosphéniques qu'à des symmétrodontes archaïques, bien que présentant des spécialisations uniques. Quelques caractères de spalacothères dérivés, tels que la perte du processus coronoïde et du sillon de meckel se développent de façon convergente chez les *Tribosphenida* et de nombreux autres groupes, et constituent des thèmes répétitifs dans l'évolution des mammifères mésozoïques. Les caractères des molaires et du dentaire suggèrent que la famille des Spalacotheriidae constitue un groupe monophylétique, le genre européen *Spalacotherium* et le genre chinois *Zhangheotherium* formant les extra-groupes successifs des autres genres. Au sein de la famille, les taxons nordaméricains semblent constituer un clade monophylétique qui culmine avec les formes hautement spécialisées comme *Symmetrodontoides* du Crétacé supérieur ; les affinités de *Microderson*, connu par un seule molaire supérieure du Crétacé du Maroc, restent énigmatiques. Les spalacotheridés étaient clairement présent en Amérique du Nord dès l'Albien-Aptien et, si l'on admet que les taxons nord-américains constituent un groupe monophylétique endémique et exclusif, leur présence sur le continent ne peut être attribuée à un éventuel échange faunique avec l'Asie au milieu du Crétacé. En revanche, les données phylogénétiques suggèrent que l'origine des Spalacotheriidae se situe en Europe occidentale au Crétacé inférieur, renforçant ainsi l'hypothèse selon laquelle il existait, à cette époque, une certaine continuité faunique entre les deux continents, hypothèse fondée initialement sur les ressemblances observées entre les faunes de dinosaures.

MOTS CLÉS
Symmetrodonta, Spalacotheriidae, phylogénie, Crétacé.

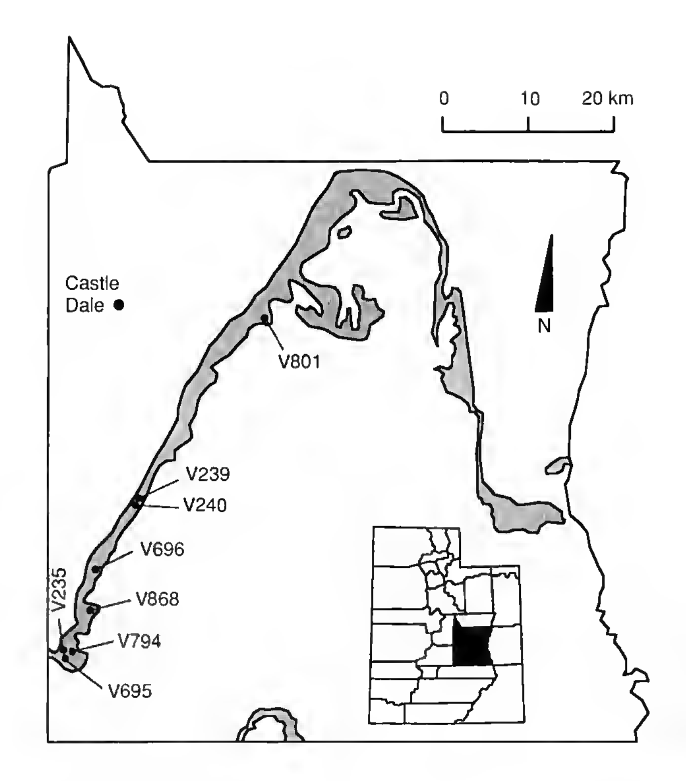


FIG. 1. — Outcrop map of the Cedar Mountain Formation, Utah (inset), and field area in Emery County. Localities are OMNH sites that produced specimens of Spalacotheriidae described in the text (see Cifelli *et al.* 1999, for sections showing stratigraphic positions of sites).

INTRODUCTION

Symmetrodonts have long been accorded a critical position in mammalian evolution because the principal cusps of upper and lower molars form the "reversed triangle" pattern that is widely believed to be morphologically intermediate between the serially tricuspid condition of triconodonts and the more elaborate molars of tribosphenic mammals (e.g., Patterson 1956). Unfortunately, their fossil record is abysmal, and they are probably the worst represented of all Mesozoic mammal "groups" (in a morphological, not taxonomic sense) – the recent discovery of an exceptional specimen from the Late Jurassic or Early Cretaceous of China (Hu *et al.* 1997, 1998) notwithstanding. Given the fact that knowledge of symmetrodont diversity and morphology is poor, it is unsurprising that they are generally omitted from comprehensive analyses of mammalian phylogeny (e.g., Rowe 1988; Wible 1991; Wible & Hopson 1993; Rougier *et al.* 1996), notable exceptions being the works of Prothero (1981) and Hu *et al.* (1997). In North America, symmetrodonts were long known from the Late Jurassic only, as represented by *Tinodon* Marsh, 1879 and the probably synonymous *Eurylambda* Simpson, 1929 (see Simpson 1929; Crompton & Jenkins 1967; Prothero 1981). Later discoveries recorded the survival of apparent "acute-angled" spalacotheriids, hitherto represented only in what was then considered the Jurassic of England, in the Early Cretaceous of Texas (Patterson 1955, 1956) and the Late Cretaceous of Alberta (Fox 1972, 1976, 1985) and southern Utah (Cifelli & Madsen 1986; Cifelli 1990). *Mictodon* Fox, 1984, an apparently relictual taxon from the Campanian of western Canada, represents the only record of an "obtuse-angled" symmetrodont from the Cretaceous of North America (Fox 1984b).

Herein we describe new taxa of intermediate age between these Early and Late Cretaceous records in North America. One of the taxa, at least, is represented by an unusually comprehensive series, affording the opportunity to examine variation and positional changes in the molar

series, and presenting new information on the dentary of advanced Spalacotheriidae. Finally, we briefly comment on the status and placement of the Spalacotheriidae with respect to other symmetrodonts and to more advanced mammal groups, and provide an hypothesis of relationships within Spalacotheriidae.

The symmetrodonts described herein were collected from the Cedar Mountain Formation, Emery County, Utah. This unit was named for a series of terrigenous sedimentary rocks lying between the Upper Jurassic Morrison Formation and the Upper Cretaceous Dakota Formation (Stokes 1944, 1952), and is broadly exposed in central and eastern Utah (Fig. 1). Five units (in ascending order) of the formation are now recognized: the Buckhorn Conglomerate, and the Yellow Cat, Poison Strip Sandstone, Ruby Ranch, and Mussentuchit members (Kirkland *et al.* 1997). The symmetrodont specimens resulted from a concerted collecting effort in a restricted stratigraphic interval of the uppermost unit, the Mussentuchit Member, 10-20 m below the contact with the overlying Dakota Formation. The specimens described herein derive from eight sites (Fig. 1); the vast majority were collected from OMNH locality V695. The fossil horizon at this locality is directly overlain by a volcanic ash. Multiple, concordant $^{40}Ar/^{39}Ar$ determinations on sanidine phenocrysts from this ash, and from the same horizon nearby, yield a date of 98.39 ± 0.07 Ma (Cifelli *et al.* 1997); hence, the fauna is indistinguishable in age from the Albian-Cenomanian (Early-Late Cretaceous) boundary, placed at 98.5 ± 0.5 Ma by Obradovich (1993) and at 98.9 ± 0.6 Ma by Gradstein *et al.* (1995). Stratigraphic sections showing placement of the principal fossil localities are given in Cifelli *et al.* (in press).

The vertebrate assemblage from the upper part of the Cedar Mountain Formation, termed the Mussentuchit local fauna, is known by more than 5000 specimens representing about 80 taxa (Cifelli *et al.* 1999). Of the mammals, only the marsupial or near-marsupial *Kokopellia* Cifelli, 1993 (see Cifelli 1993; Cifelli & Muizon 1997), three triconodontids (Cifelli & Madsen 1998), and several multituberculates (Eaton & Nelson 1991) have been described thus far.

METHODS

Specimens were recovered using a combination of standard quarry procedures, through which most of the dentulous jaw fragments and a few of the larger isolated teeth were recovered, coupled with a large-scale underwater screenwashing operation (Cifelli *et al.* 1996; Madsen 1996). It is worthwhile pointing out that most of the isolated teeth were recovered from the fine fraction of internested screen boxes, in which the corresponding screen size was 30-mesh; had only window screen been employed, as is common practice for Late Cretaceous rocks of the US, few of these specimens (most of which have a maximum dimension of significantly less than 1 mm) would have been recovered.

Measurements were taken with a Reflex microscope, which permits non-contact recording of point coordinates in three dimensions; minimum standard errors are two microns on the x, y-axes and five microns on the z-axis (MacLarnon 1989). Reflex data are automatically recorded to 0.001 mm, and these data are reproduced verbatim here, although we point out that this does not take into account measurement error (see Lillegraven & Bieber 1986).

Measurements are shown in Figure 2. Spalacotheriid molars are extremely small and fragile; the lower molar cingula are particularly vulnerable to breakage. In order to maximize sample size for lower molars, we took standard length and width measurements minus the cingulum. We remeasured specimens of other relevant Spalacotheriidae using the same procedure; measurements of *Spalacotheroides bridwelli* Patterson, 1955 are from an epoxy cast, and those of *Symmetrodontoides canadensis* Fox, 1976 are from Fox (1976, fig. 5; 1985, fig. 1). Other measurements were taken by defining points at the apices of the primary cusps (paraconid, protoconid, metaconid) and calculating: (1) the distances between them; (2) the angle (herein called trigonid angle) formed between the points, with the protoconid at the apex. The trigonid angle is rather variable, even among teeth of the same locus. Consideration of tooth morphology suggests that the trigonid angle decreases with wear: the mesial and distal faces of the paraconid and

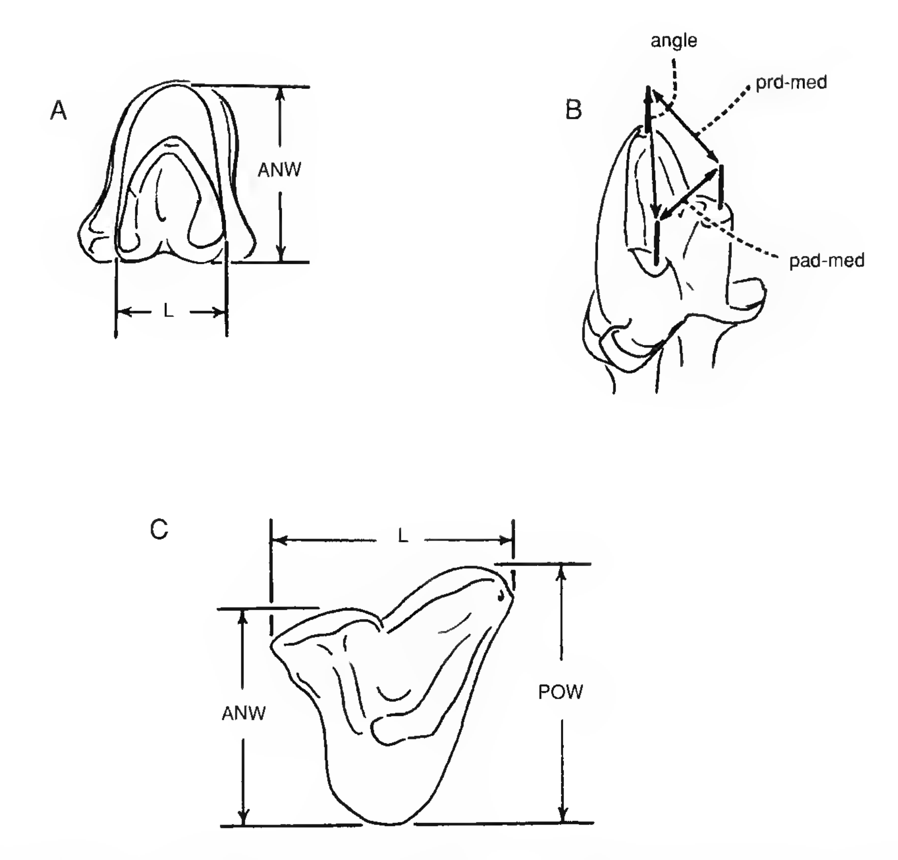


FIG. 2. — Spalacotheriid molars showing measurement conventions; **A**, right lower molar, occlusal view; **B**, right lower molar oblique occlusolingual view; **C**, left upper molar, occlusal view. Abbreviations: **angle**, angle formed by lines connecting apices of paraconid to protoconid and metaconid to protoconid; **ANW**, anterior width (greatest width of lower molars); **L**, mesodistal length; **pad-med**, distance from apex of paraconid to apex of metaconid; **POW**, posterior width; **prd-med**, distance from apex of protoconid to apex of metaconid.

metaconid (respectively) are rather vertical, whereas their opposing faces slope downward toward each other, so that the apparent centers of the cusps will migrate toward each other as wear progresses. We also attempted to take height measurements. However, our efforts were frustrated by our inability to define a repeatable plane of reference, and the fact that wear varies considerably from one specimen to the next. Hence, references to difference in crown height are qualitative only. For upper molars, we took measurements (Fig. 2) analogous to those employed for tribosphenic therians (see Lillegraven 1969, fig. 5). Calculations, descriptive statistics, and tests were done with Systat version 7; original data are available from the senior author upon request.

Dental terminology is shown in Figure 3. The homologies of some of the upper molar cusps of spalacotheriids and other symmetrodonts – e.g., the presence of a metacone (Butler 1939; Patterson 1956) – are unclear, and the nomenclature is inconsistent. Most workers have referred to the three primary cusps of upper and lower molars in primitive mammals as A, B, and C; and a, b, and c, respectively (e.g., Crompton & Jenkins 1968; Cassiliano & Clemens 1979; Jenkins & Crompton 1979). Crompton (1971) regarded the metacone of tribosphenic Theria as a neomorph, and referred to the distolabial of the three primary upper molar cusps as cusp "c"; we follow convention in referring to this as cusp C, in order to avoid confusion with lower molar cusp c, though we point out that similar problems exist with this term, as upper molars of primitive marsupials and certain other tribo-

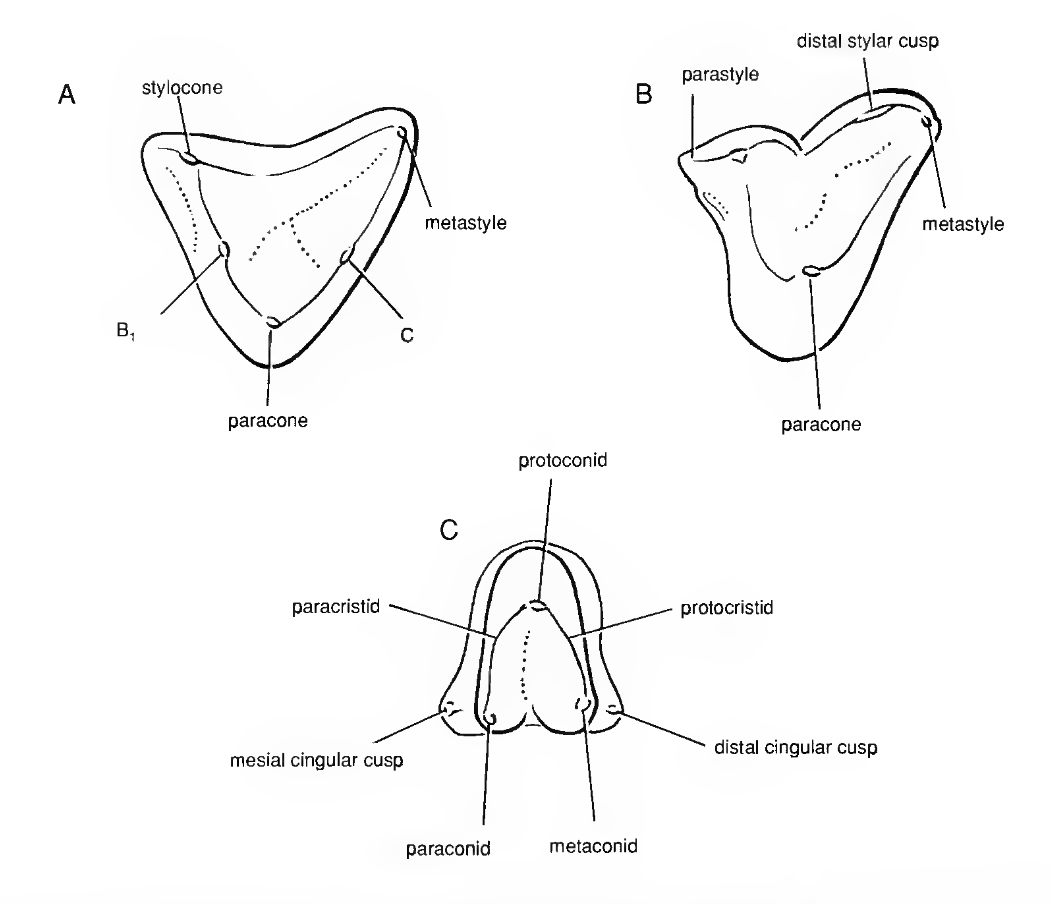


FIG. 3. — Dental terminology employed in this paper ; **A**, upper molar (M4) of *Spalacotherium* (modified after Simpson 1928a, fig. 34, and Patterson 1956, fig. 12); **B**, upper molar of *Spalacolestes*; **C**, lower molar of *Spalacolestes*.

sphenic mammals have a stylar cusp C (see Clemens 1979, we thank R. C. Fox for pointing this out to us). Other authors (Butler 1939; Patterson 1956; Kermack *et al.* 1968; Prothero 1981; Hopson 1997) interpret cusp C – which in spalacotheriids (where present) is located on the postparacrista about midway between the paracone and the distolabial corner of the tooth – as homologous with the tribosphenidan metacone. Following arguments presented by Sigogneau-Russell & Ensom (1998), we believe this to be probable, but follow Hu *et al.* (1998) in retaining the traditional nomenclature for spalacotheriids. Certain spalacotheriids also have an unusual cusp on the preparacrista, about halfway between the paracone and the mesolabial corner of the tooth, where a second cusp is generally present. We follow Patterson (1956) and Sigogneau-Russell & Ensom (1998) in regarding the latter cusp as the stylocone (see also Sigogneau-Russell 1991a), so that the cusp lingual to it (but labial to the paracone) is a neomorph. The most recently applied term for this cusp in the middle of the preparacrista is cusp B_1 (Hu *et al.* 1997), and this usage is adopted herein. Symmetrodont upper molars also commonly bear one or more cusps placed on the stylar shelf, distal to the ectoflexus (if one is present). That at the corner of the tooth may be termed, by convention, the metastyle. The more mesially placed cusp has been referred to as a posterior stylar cusp (e.g., Fox 1985) or, in analogy with the similarly placed cusp of tribosphenic therians (e.g., Simpson 1929; Clemens 1979; Fox 1984a), as stylar cusp D (e.g., Sigogneau-Russell 1991b; Sigogneau-Russell &

Ensom 1998). Unfortunately, the term "cusp D" has also been applied to the metastylar cusp (Hu *et al.* 1997). In order to avoid confusion with this usage or implied homology with the similarly-positioned cusp of marsupials, placentals, or therians of "metatherian-eutherian grade," we refer to the cusp placed on the stylar shelf, distal to the median part of the tooth but proximal to the metastyle (with which it should not be confused), as a "distal stylar cusp."

The medial surface of the dentary in mammals commonly bears a ridge, crest, or analogous structure, generally near or at the inferior margin and located posterior to the mandibular foramen, for attachment of the m. pterygoideus medialis. We are unable to find a standard anatomical term for this structure, and various names have been applied to it in the literature. Simpson (e.g., 1926, 1928a) alternatively referred to this structure as a "pterygoid crest" or "pterygoid ridge," sometimes using both terms in the same work (e.g., Simpson 1929). Recent authors (e.g., Rowe 1988) sometimes refer to it as a "pterygoid shelf," and this term has become standard for multituberculates (e.g., Miao 1988; Gambarayan & Kielan-Jaworowska 1995), in which the inferior margin of the dentary is strongly inflected lingually. In order to promote precision in usage and to avoid confusion in character state or implied homology (see discussion in Miao 1993), we refer to the structure in question simply as a "pterygoid crest," except where it is obviously developed into a shelf, as in multituberculates, or into an inflected angle, as in marsupials and some early Eutheria (see Sánchez-Villagra & Smith 1997, and below). At least, one of the species described herein is characterized by a pterygoid crest that bears a hypertrophied, process-like lingual extension that is unique, so far as we are aware. Lacking any standard term for this feature, we refer to it as a "pterygoid process."

ABBREVIATIONS FOR INSTITUTIONS CITED IN THE TEXT

BM	British Museum, London, UK;
UK	FMNH, Field Museum of Natural History, Chicago, Illinois, USA;
GI PST	Institute of Geology, Section of Palaeontology and Stratigraphy, Mongolian Academy of Sciences, Ulan Bator, Mogolian Peoples' Republic;
MNA	Museum of Northern Arizona, Flagstaff, Arizona, USA;
OMNH	Oklahoma Museum of Natural History, Norman, Oklahoma, USA;
UALVP	University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA;
YPM	Yale Peabody Museum, New Haven, Connecticut, USA.

SYSTEMATIC PALEONTOLOGY

Order SYMMETRODONTA Simpson, 1925

COMMENTS. — This group was proposed by Simpson (1925a) to include then-known taxa (all thought to be Jurassic in age) having the three principal molar cusps arranged in a triangular pattern, thereby distinguishing them from the serially tricuspid triconodonts, with which they had been previously grouped (e.g., Osborn 1888, 1907). Symmetrodonta have long been conceived as a paraphyletic group (see, e.g., Patterson 1956; Cassiliano & Clemens 1979, fig. 7-4), but this simple picture became increasingly complex with the discovery of geologically older taxa, particularly Rhaeto-Liassic *Kuehneotherium* Kermack *et al.*, 1968 (see Kermack *et al.* 1968) and, later, *Woutersia* Sigogneau-Russell, 1983 (see Sigogneau-Russell 1983; Sigogneau-Russell & Hahn 1995). Mandibles referred to *Kuehneotherium*, at least, retain a postdentary trough and attachment facets for the postdentary elements seen in cynodonts and primitive mammals such as *Morganucodon* Kühne, 1949 and docodonts (Kermack & Mussett 1958; Kermack *et al.* 1968; Kermack *et al.* 1973; Lillegraven & Krusat 1991), and lack derived features (such as a pterygoid crest) found in other mammals, including some triconodonts (e.g., Rowe 1988; Wible 1991; Wible & Hopson 1993). Hence, either the mammalian middle ear complex or the "reversed triangle" pattern of upper and lower molars evolved independently more than once; both cases have been argued (see, e.g., Allin & Hopson 1992; Rougier *et al.* 1996). Prothero (1981) resolved this problem by excluding *Kuehneotherium* from Symmetrodonta (see also Hopson 1994), but his analysis did not include non-therian groups, and it is unclear how other, more recently described taxa (e.g., *Woutersia*, *Zhangheotherium* Hu *et al.*, 1997, *Thereuodon* Sigogneau-Russell, 1989, *Shuotherium* Chow & Rich, 1982, *Kotatherium* Datta, 1981, and a host of enigmatic taxa from the Campanian Los

Alamitos fauna of Argentina: see references cited above and Datta 1981; Chow & Rich 1982; Sigogneau-Russell 1989; Bonaparte 1990; Sigogneau-Russell 1991b; Prasad & Manhas 1997; Sigogneau-Russell & Ensom 1998) would fit into this scheme. The situation is further complicated by the fact that some molars of Amphilestidae, generally placed in the Triconodonta (e.g., Simpson 1945), have their principal cusps arranged in an obtuse triangle, and a relationship to Symmetrodonta has been suggested on this basis (Mills 1971; see also Jenkins & Schaff 1988; and discussion in Kielan-Jaworowska & Dashzeveg 1998). Fox (1985) proposed a trifold classification of Symmetrodonta, including Tinodontidae (containing *Kuehneotherium* and several other taxa, as well as *Tinodon*). *Kuehneotherium* has been shown to be highly similar to *Tinodon* (e.g., Crompton & Jenkins 1967), but its placement in the Tinodontidae is plagued by the same difficulty as its referral to Symmetrodonta in general: it retains an extremely primitive jaw structure, whereas in *Tinodon* the postdentary elements were evidently detached and a pterygoid crest is present (see Prothero 1981). We can offer nothing new to solve this dilemma and thus have not attempted to define or diagnose Symmetrodonta. However, there are some data to uphold integrity of the "core" group, Spalacotheriidae. Pending further analysis and, hopefully, more data from the fossil record, we find it useful to retain a traditional, inclusive concept of "symmetrodonts" (e.g., Cassiliano & Clemens 1979; Fox 1985). A recent, comprehensive discussion of the problem in defining Symmetrodonta, together with a thorough historical review of relevant taxa, is given by Sigogneau-Russell & Ensom (1998). McKenna & Bell (1997) distributed the contents of the Symmetrodonta among several higher groups within Mammalia, which they diagnosed primarily on the basis of detachment of accessory jaw bones (postdentary complex) from the craniomandibular joint and their association with the cranium as elements of the auditory apparatus. This arrangement implies a reversal for *Kuehneotherium* which, as noted, evidently retained a full complement of postdentary elements that were well integrated with the dentary.

Recently, the term "Theria" has been formally defined as a crown-based taxon restricted to the common ancestor of marsupials, placentals, and all of its descendants (Rowe 1988). Herein we follow a more traditional, informal concept that also includes "Theria of metatherian-eutherian grade," peramurans, eupantotheres, and symmetrodonts (e.g., Patterson 1956), in recognition of the current instability in phylogenetic interpretation of the major groups of mammals.

Family SPALACOTHERIIDAE Marsh, 1887

TYPE GENUS. — *Spalacotherium* Owen, 1854.

INCLUDED GENERA. — The type, and *Spalacotheroides* Patterson, 1955; *Symmetrodontoides* Fox, 1976; *Spalacotheridium* Cifelli, 1990; *Microderson* Sigogneau-Russell, 1991; *Zhangheotherium* Hu *et al.*, 1997; and *Spalacolestes*, n. gen.

DISTRIBUTION. — ?Late Jurassic through Early Cretaceous, western Europe (Clemens 1963; Clemens & Lees 1971; Krebs 1985); Early through Late Cretaceous, North America (Patterson 1955; Fox 1976); Late Jurassic or Early Cretaceous, Asia (Hu *et al.* 1997); ?Early Cretaceous, northern Africa (Sigogneau-Russell 1991b). *Spalacotherium* was first described from the Purbeck beds, traditionally regarded as Upper Jurassic (see discussion in Clemens *et al.* 1979). Recent literature increasingly refers the mammal-bearing part of the Purbeck to the Berriasian (Lower Cretaceous, see Allen & Wimbledon 1991; Kielan-Jaworowska & Ensom 1994; Sigogneau-Russell & Ensom 1994; Ensom & Sigogneau-Russell 1998).

REVISED DIAGNOSIS. — Symmetrodonts with lower molars bearing well-developed primary cusps (paraconid, protoconid, metaconid) arranged in an acute angle, a reduced talonid; five lower molars present in *Zhangheotherium*, increasing to six or more, where known, in other taxa. Unique pattern of interlocking for lower molars, whereby the distal cingular cusp of one molar is placed labial to the mesial cingular cusp of the succeeding tooth. Upper molars primitively with accessory cusp (B_1) on preparacrista between paracone and stylocone.

COMMENTS

A more detailed diagnosis of Spalacotheriidae was given by Fox (1985), based on then-known taxa: *Spalacotherium*, *Spalacotheroides*, and *Symmetrodontoides*. The concept of the family is broadened here to include *Zhangheotherium*, recently described from the Late Jurassic or, more probably, Early Cretaceous of China (Hu *et al.* 1997). By comparison to remaining spalacotheres, *Zhangheotherium* would appear to be primitive in some respects, such as the lower number of molars, ?lack of continuous mesial and distal shearing surfaces on molars (upon eruption), and, perhaps, features on the medial side of the dentary (see below). In other respects, such as the complete lack of cingula on the lower molars, *Zhangheotherium* is strikingly atypical. Nonetheless, molar morphology is otherwise similar to that of *Spalacotherium*, particularly in the presumably derived features cited in the dia-

gnosis. We tentatively follow Hu *et al.* (1997) in referring *Zhangheotherium* to the Spalacotheriidae. Cusp B_1 is present in *Spalacotherium* (e.g., Clemens 1963), *Spalacotheroides* (see Patterson 1956), and *Zhangheotherium* (see Hu *et al.* 1997), the geologically oldest and, for reasons detailed below, considered by us to otherwise be the most primitive members of the family. We therefore tentatively regard the presence of cusp B_1 to be primitive for (and diagnostic of) Spalacotheriidae. Sigogneau-Russell & Ensom (1998) considered the loss of Crompton (1971)'s facet A as characterizing Spalacotheriidae. It is presently uncertain as to whether or not facet A is seen in *Zhangheotherium*, and this feature has accordingly been omitted from the diagnosis, pending detailed description of that taxon.

Microderson, represented by a single tooth belonging to the type and only species, *M. laaroussii* Sigogneau-Russell, 1991, from the Early Cretaceous of Morocco, was initially described as a spalacotheriid (Sigogneau-Russell 1991b), but its pertinence to the family has recently been called into question (Sigogneau-Russell & Ensom 1998). We tentatively include it here for the sake of completeness but, because it is poorly known and of enigmatic affinities, make only passing reference to it in the comparisons below.

Given the low known diversity of symmetrodonts and their meager representation in the fossil record, it comes as somewhat of a surprise that several species, collectively represented by more than 250 specimens, are present in the Mussentuchit local fauna. Most of these specimens are isolated teeth, many of which are worn or incomplete. This, coupled with the facts that the species are quite similar to each other and to named taxa from North America, that the tooth rows include many molars (probably seven in the lower series and six in the upper series) that are rather simple and vary in only subtle ways from one position to the next, and that no closely similar taxon is known by anything close to a complete dentition, makes identification of taxon and tooth position less than straightforward (see also Mills 1984). We gave first consider-ation in our analyses to the lower molar series for several reasons. First, the sample of lower molars is comparatively large, thus permitting statistical treatment and some appraisal of variability. Second, the most morphologically informative specimens, both from the Cedar Mountain Formation and elsewhere (e.g., Fox 1976), are dentigerous mandibular fragments. A final, most compelling reason for giving primary consider-ation to the lower molars is that the holotypes of all spalacotheriid symmetrodonts (except *Microderson*) include lower molars, and most species are based on lower molar series or individual teeth.

The less numerous upper molars were then assigned to lower molar taxa based on size and morphological considerations, and were sorted to locus (see below). Judged from the composition of the Mussentuchit local fauna (Cifelli *et al.* 1997, 1999) and comparison with *Spalacotherium* (see Simpson 1928a), spalacotheriid premolars are clearly present in the existing collection. No attempt was made to sort these according to taxon, however, because of the difficulties posed by assignment to locus; hence, only the molar dentition is considered herein.

Lower molars

Fortunately, one of the taxa from the Cedar Mountain Formation is known by a relatively enormous sample; several jaws are included, and as a result the last four molar loci of the mandibular dentition are represented by teeth in place. A dentary fragment preserving the anterior part of the molar series, including three loci, is known for the closely similar *Symmetrodontoides canadensis* (see Fox 1972, 1976). These specimens, together with comparison to the complete dentition of the somewhat more divergent *Spalacotherium* (see Simpson 1928a; Clemens 1963), provide the foundation for evaluating position of isolated teeth on the basis of relative crown height, differences in the proportions of the lingual cusps (paraconid, metaconid), acuteness of the trigonid angle, configuration of the lingual cingulum, width to length proportions, and other considerations.

Once the lower molars were sorted to their relative and approximate positions in the tooth row, it became apparent that three diagnosable species, differing in size (Fig. 4) and morphology, were

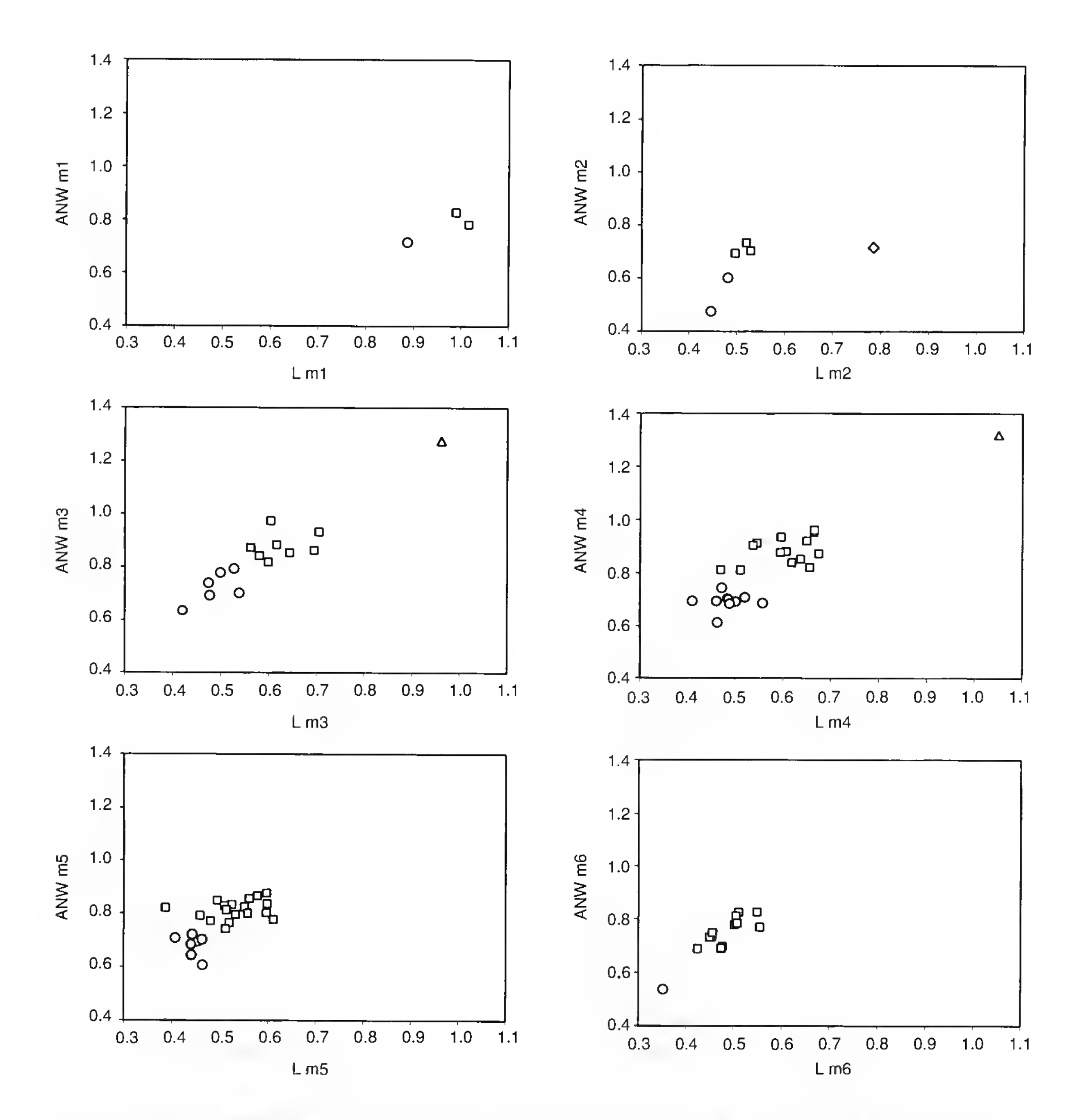


Fig. 4. — Bivariate scatterplots for lower molar length (**L**) and width (**ANW**) of Spalacotheriidae from the upper Cedar Mountain Formation by inferred tooth locus. Symbols: **circles**, *Spalacotheridium noblei* n. sp.; **squares**, *Spalacolestes cretulablatta* n. gen., n. sp.; **triangles**, *Spalacolestes inconcinnus* n. gen., n. sp.; **diamond**, gen. and sp. indet.

present in the sample: the well-represented taxon just mentioned, known by several jaws and nearly 100 isolated molars; a smaller species, represented by about 35 isolated teeth; and a larger species, for which only three lower molars are known. One problematic specimen evidently represents a fourth, unidentified taxon. For the species represented by the largest sample, it was then possible to conduct detailed comparisons in order to identify tooth locus more precisely, evaluate variability at each tooth position and differences between adjacent teeth (in terms of their

measurements), and estimate the molar count. These results were then used for refinement of identifications for the other species. Description of the results is deferred to the individual species accounts, but some prefatory comments are warranted here because of the need to provide a basis for comparison with previously described species, and the implications of the results presented herein for interpretation of tooth position among specimens referred to those species.

As mentioned, the best-represented spalacotheriid of the Mussentuchit local fauna is known by the last four lower molars in place, as well as by a large sample of isolated teeth. Except for the last molar, which is morphologically distinctive, it is not possible to identify positions of individual posterior molars with certainty because of overlapping ranges of variation between loci. Nonetheless, the isolated molars fall into recognizable clusters corresponding to known tooth positions, and we consider our identifications to be probable, with mistaken identity by more than one tooth position being unlikely.

Among the isolated teeth representing anterior molar loci, one group is consistently and clearly recognizable. Based on known trends in the dentition of spalacotheriids (e.g., Simpson 1925b, 1928b; Clemens 1963; Fox 1976), these teeth can be confidently identified as m1. The teeth that are morphologically intermediate between this first molar and the anteriormost of those in known tooth positions fall into two clusters, recognizable on the basis of both qualitative and quantitative characteristics. Again, however, because of overlapping ranges of variability, individual teeth can be identified with probability, not certainty, according to position. Hence the available data indicate that, in this species at least, seven lower molars were present. Rather than using quotation or question marks on the numerous specimens cited below, we simply call attention to the facts that a complete dentition of a North American spalacotheriid remains unknown and that, in any case, identification of isolated molars (except the first and last, which are morphologically distinctive) cannot be established unambiguously, even with complete specimens at hand for comparison. The identifications of teeth to respective loci should be regarded as tentative.

Of the remaining spalacotheriids from the Mussentuchit local fauna, comparison with the taxon just mentioned indicated that a second species is represented by teeth recognizable as belonging to the first six lower molar positions; these will be referred to as m1-6. It is unclear as to whether an m7 was lacking in this species, or is not represented in existing collections. The third diagnosable species is known by only three lower molars, each recognizable as to locus with the same confidence as the morphologically similar, best-represented species.

Among described species of North American Spalacotheriidae, the best known is *Symmetrodontoides canadensis*, the holotype of which (UA 8588) consists of an incomplete jaw with three teeth. These were identified by Fox (1976) as probably representing m3-5. The basis for this identification was a referred specimen, UA 12086, a mandibular fragment with a molariform tooth considered to be m1. The tooth of UA 12086 has a broadly obtuse trigonid angle that, if compared to UA 8588, would form a graded series with the teeth on the latter specimen, assuming that an unrepresented tooth position intervened between the two specimens. Dentigerous jaws and numerous isolated teeth similar to that of UA 12086 are known from the Cedar Mountain Formation, and work in progress by one of us (RLC) indicates that these are not lower molars of spalacotheriids. Comparison of UA 8588 to the extensive series mentioned above indicates that the teeth in this specimen are m1-3. Fox (1976) also referred an isolated molar, UA 12087, to *Symmetrodontoides canadensis*. As demonstrated by Fox, this tooth clearly represents a more posterior tooth locus. Consideration of the proportional differences between this specimen and m3 of the holotype, together with the large sample from the Cedar Mountain Formation, suggests that UA 12087 probably is an m5 or, as Fox (1976) suggested, m6.

Other species are known by isolated teeth only, and identification of tooth position is more problematic. The first symmetrodont to be described from the Cretaceous of North America is *Spalacotheroides bridwelli*, from the Aptian-Albian of the Trinity Group, Texas. *S. bridwelli*

was based on a mandibular fragment with a single lower molar (Patterson 1955); several upper molars were later referred to the species (Patterson 1956). Patterson (1955) suggested that, as with *Spalacotherium*, *Spalacotheroides* probably had seven molars, and that the tooth in the holotype (FMNH PM 933) is the antepenultimate – i.e., m5. Fox (1976) indicated that this tooth best matches the second tooth on the holotype of *Symmetrodontoides canadensis*, then identified as m3 or 4 and considered herein to be m2. We concur: in terms of size and overall morphology, we find FMNH PM 933 to be most similar to m2 or 3 of *Symmetrodontoides*. However, the paraconid on FMNH PM 933 is lacking. For this reason, and because tooth locus cannot be reasonably hypothesized without other specimens belonging to the same species, the lower dentition of *Spalacotheroides bridwelli* must be set aside from comparisons for the time being. This species is said to differ from *Spalacotherium* (see Patterson 1955) and all other Spalacotheriidae (Fox 1976) except *Zhangheotherium* in having an incomplete labial cingulum. No other lower molars are yet known for *S. bridwelli*. A somewhat more obtuse-angled tooth (perhaps m1), comparable in size and overall gestalt to FMNH PM 933, is now known from the Cloverly Formation (RLC, unpublished data), which is approximately equivalent in age to the part of the Trinity Group that produced *Spalacotheroides* (Jacobs *et al.* 1991). Unfortunately, the labial side of this tooth is damaged, leaving open the question of whether or not the cingulum was complete.

Three species of Spalacotheriidae have been described from the Upper Cretaceous of southern Utah. *Symmetrodontoides foxi* Cifelli & Madsen, 1986, from the Wahweap Formation (assumed to be lower Campanian and approximately equivalent to the upper Milk River Formation, Alberta, which produced *S. canadensis*), was based on presumed m4 (MNA 4589, the holotype) and a referred tooth (MNA 4522) assumed to represent m7 (Cifelli & Madsen 1986). A new specimen of this species, together with comparison to the extensive series representing a morphologically similar species from the Cedar Mountain Formation, suggests that MNA 4589 is an m2 and that MNA 4522 is m6 (or, less probably, m5); m4 of *S. foxi* is represented by OMNH 20135.

The Smoky Hollow Member of the Straight Cliffs Formation, late Turonian in age (Eaton 1991), has yielded two spalacotheriids (Cifelli 1990). The present comparisons, which include new materials, indicate that the holotype of *Symmetrodontoides oligodontus* Cifelli, 1990 (MNA 5789) is probably m6 (not m7 as originally thought), and that the original referred specimen (OMNH 20381) represents m4. Newly-referred specimens include MNA 6047 and 6755, tentatively identified as m2 and m4, respectively; and 29523, a mandibular fragment with m2. The holotype of the diminutive *Spalacotheridium mckennai* Cifelli, 1990 is most probably m2 (not m4 as originally believed); newly-referred OMNH 29524, MNA 6046, and OMNH 29526 are probably m1, m4, and corroded m6, respectively.

Upper molars

The upper molars are evidently much more fragile and subject to breakage during the screenwashing process: the sample from the Cedar Mountain Formation includes only 54 catalogued upper molars, as opposed to more than 200 lowers. Of these, 45 upper molars proved assignable to species but only 31 were formally included in hypodigms because of their greater completeness; statistical analysis was precluded by insufficient samples. With one exception (described under ?Spalacotheriidae, indet.), the upper molars readily fell into three categories on the basis of size, as had been established for the lower molars. Within species, there is variation that is clearly due to tooth locus. Trends known for symmetrodonts represented by dentulous jaws (e.g., *Spalacotherium*, *Zhangheotherium*, see Simpson 1928b; Clemens 1963; Hu *et al.* 1997), together with molars (Fox 1985) of a species similar to those from the Cedar Mountain Formation, provided the basis for establishing which teeth were more anteriorly placed in the jaw, and which of these represented the first molar. For the most abundant species, it was then possible to sort molars into discrete morphological categories, and to document progres-

sive changes through the upper series. We recognize six morphological categories among upper molars of this species, and therefore tentatively regard the upper molar count as six. This accords with the fact that, in the lower dentition, where we believe seven molars are present, m7 is reduced and has a prevallid (for shearing against the distal face of M6) but no postvallid surface. A differential molar count between upper and lower jaws is not wholly unexpected, as the condition is known to occur in the primitive spalacotheriid *Zhangheotherium* (see Hu *et al.* 1997). Simpson (1928a) regarded the upper dentition of *Peralestes* (which we include in *Spalacotherium*) as having seven molars. Clemens (1963) later showed that only six were present on one specimen, at least; it is possible that molar count varied in this taxon.

Identification of upper molars belonging to the most abundant species then served as the basis for identifying loci among isolated teeth referable to the less abundant taxa from the Cedar Mountain Formation, and for morphologically similar species from elsewhere. Fox (1985) referred two upper molars to the Aquilan spalacotheriid *Symmetrodontoides canadensis* and indicated that one probably represents a more posterior locus than the other. We find this indeed to be the case, our comparisons suggesting that UALVP 16271 is M1 or 2 and UALVP 16272 is M2 or 3 of this species. No upper molars have yet been described for symmetrodonts from southern Utah, but materials in hand suggest that the following are represented: *Symmetrodontoides foxi*, M4 (MNA V4653); *S. oligodontos*, M1 (OMNH 29525), M2 (MNA V6048, OMNH 29040), and M6 (OMNH 29039); *Spalacotheridium mckennai*, M5 (MNA V6756). Other spalacotheriids for which isolated upper molars have been described are problematic because only single teeth (rather than series) are available, and they are so different from the taxa considered here as to be non-comparable. Several isolated upper molars have been referred to *Spalacotheroides bridwelli*. Of these, FMNH PM 1235 is relatively long mesiodistally and probably represents an anterior position, as indicated by Patterson (1956, fig. 1). A cast of FMNH PM 1133, which is just a fragment of a tooth, suggests that this may have been a more posterior molar. The upper molar series is known for *Zhangheotherium*; however, the preliminary description and available illustration (which shows the upper molars in an oblique orientation, Hu *et al.* 1997, fig. 2) permit only cursory comparisons with remaining spalacotheriids. The remaining taxon possibly referable to Spalacotheriidae and represented by an isolated upper molar is *Microderson laaroussii*, from the Early Cretaceous of Morocco. As recognized by Sigogneau-Russell (1991b), this tooth is so dissimilar to upper molars of *Symmetrodontoides* (and, by implication, to remaining taxa considered here) that we cannot hazard a guess as to its position in the jaw.

SPALACOLESTINAE n. subfam.

TYPE GENUS. — *Spalacolestes*, n. gen.

INCLUDED GENERA. — The type, and *Spalacotheroides* Patterson, 1955, *Symmetrodontoides* Fox, 1976, and *Spalacotheridium* Cifelli, 1990.

DISTRIBUTION. — Cretaceous (Aptian-Albian through early Campanian), North America.

DIAGNOSIS. — Distinguished from primitive spalacotheriids (*Spalacotherium*, *Zhangheotherium*) in possessing the following derived features: molars more acutely angled; anterior upper molars with strong parastyle; upper molars with preparacrista lower than postparacrista and with distal stylar cusp present, proximal to the metastyle. Pterygoid crest and pterygoid fossa, where known (*Spalacolestes*, *Spalacotheroides*) extend anterodorsally from mandibular foramen toward alveolar margin of dentary.

COMMENTS. — As shown by the comparisons below, there is good reason to believe that the North American Cretaceous spalacotheriids form a monophyletic assemblage with respect to remaining members of the family. We formalize this relationship by placing the North American taxa in their own subfamily, named for the best known genus (described below). Within the subfamily, poorly known *Spalacotheroides* is the oldest and appears to retain the greatest number of primitive features. The remaining genera of Spalacotheriidae (*Spalacotherium*, *Zhangheo-*

therium), not treated in detail herein, are relegated, by default, to Spalacotheriinae (Marsh 1887), n. rank, which current evidence suggests may be paraphyletic (see below).

Spalacolestes n. gen.

TYPE SPECIES. — *Spalacolestes cretulablatta* n. sp.

INCLUDED SPECIES. — The type, and *S. inconcinnus* n. sp.

ETYMOLOGY. — *Spalax* (Greek), mole, and a commonly used prefix for genera of this family; *lestes* (Greek), robber, plunderer, and a commonly used suffix for genera of small and presumably stealthy, predaceous mammals.

DISTRIBUTION. — Albian-Cenomanian, western United States.

DIAGNOSIS. — Differs from *Spalacotherium* in having more acutely angled trigonids on posterior molars and in having lower molar paraconid much lower than metaconid. Differs from *Symmetrodontoides* in having proportionately narrower posterior lower molars with more obtusely-angled trigonids and lesser height differential between paraconid and metaconid; m1 differs from that of *Symmetrodontoides* in having lower, more conical paraconid and lower paractistid. Lower molars differ from those of *Spalacotheridium* in having a more pronounced height differential between paraconid and metaconid. Upper molars similar, where known, to those of *Symmetrodontoides*, except that M1-2 have a more bulbous-based paracone with a gently curving (not tightly arced or folded) lingual face. Upper molars differ from those of *Spalacotheroides* and primitive taxa in reduction of the stylocone, lack of cusps B_1 and C, presence of an extremely low preparactista (anterior loci only), and presence of an enlarged distal stylar cusp. Differs from the otherwise similar *Spalacotheridium* in having deeper trigon basins and, on posterior upper molars, parastyle reduced.

Spalacolestes cretulablatta n. sp.
(Figs 6-11)

HOLOTYPE. — OMNH 29600, right dentary with m4-7.

HYPODIGM. — The holotype, and the following specimens:
Jaws: dentary with m4-5, OMNH 27421; dentary with m6, OMNH 27557.
Lower molars: **m1**, OMNH 26424, 26425, 26697, 29608, 30621, 33044, 33220; **m2**, OMNH 27451, 27511, 27541, 32947, 33045, 33054, 33226, 33898; **m3**, OMNH 26698, 27591, 27631, 33047, 33217, 33851; **m4**, OMNH 26419, 26420, 26422, 26704, 26708, 27471, 27484, 27630, 30627, 30628, 30631, 33055, 33225, 33901; **m5**, OMNH 26423, 26695, 26703, 26706, 26707, 27462, 29603, 29606, 30619, 30620, 33037, 33042, 33043, 33049, 33050, 33222, 33905; **m6**, OMNH 27425, 27464, 27569, 29601, 29767, 30622, 30625, 33040, 33046, 33048, 33218, 33228; **m7**, OMNH 27463.
Upper molars: **M1**, OMNH 26426, 33233; **M2**, OMNH 26686, 29611, 32897; **M3**, OMNH 27512, 33060; **M4**, OMNH 26688, 26693, 30611, 30612, 33057, 33231; **M5**, OMNH 25796; **M6**, OMNH 26691, 30614, 32949.

ADDITIONAL REFERRED SPECIMENS. — Incomplete upper molars, locus uncertain: OMNH 25795, 26427, 26430, 27632, 33056, 33058, 33059, 33235, 33237, 33906, 33907.

LOCALITIES AND HORIZON. — OMNH localities V235, V239, V695, V794, and V868 (Fig. 1); upper part of Cedar Mountain Formation; Albian-Cenomanian.

ETYMOLOGY. — *Cretula* (Latin, dim. of *creta*), chalk; *blatta* (Latin), cockroach. Allusion is to the Cretaceous age and remarkable, roach-like abundance of the species.

DIAGNOSIS. — The smaller of the two species referred to the genus. Differs from the slightly smaller *Symmetrodontoides oligodontos* in characters noted for generic diagnosis and in having less slender, anteroposteriorly compressed lower molar para- and metaconids. Differs from *S. foxi* and *S. canadensis* in generic charactets and in being much smaller.

COMMENTS AND DESCRIPTION

Lower molar series

Spalacolestes cretulablatta n. gen., n. sp. is the most abundant therian mammal of the Mussentuchit local fauna and is represented by 94 specimens of the lower molar series. Of these, the holotype preserves the last four molars in place, and two other dentulous jaws have teeth of known position in the posterior part of the series. Isolated teeth not referable to these loci can be sorted into three groups based on crown height, relative height and position of the paraconid, curvature of the lingual cingulum, and other characteristics. Standard measurements for these teeth (Table 1) also group into distinct clusters; as noted above, we therefore recognize seven lower molars. The most morphologically

TABLE 1. — Descriptive statistics for lower molar measurements (mm) of *Spalacolestes cretulablatta* n. gen., n. sp. See Figure 2 for measurement abbreviations and conventions.

	L	ANW	Pad-med	Prd-med	Angle
m1					
N	2	7	2	3	2
Range	0.989-1.016	0.750-0.856	0.730-0.750	0.559-0.716	61.771-68.440
Mean	1.002	0.801	0.740	0.652	65.106
CV	0.019	0.052	0.019	0.126	0.072
m2					
N	3	4	4	3	3
Range	0.496-0.529	0.694-0.752	0.431-0.444	0.415-0.480	45.600-50.309
Mean	0.515	0.721	0.437	0.448	48.163
CV	0.033	0.037	0.015	0.073	0.049
m3					
N	8	10	8	8	7
Range	0.562-0.705	0.809-0.975	0.369-0.552	0.498-0.663	42.738-48.260
Mean	0.626	0.878	0.473	0.562	45.950
CV	0.083	0.059	0.113	0.099	0.051
m4					
N	14	16	11	12	11
Range	0.470-0.675	0.736-0.963	0.359-0.472	0.496-0.598	29.714-40.046
Mean	0.601	0.868	0.413	0.598	35.068
CV	0.106	0.075	0.087	0.086	0.094
m5					
N	18	19	12	14	10
Range	0.387-0.612	0.742-0.876	0.362-0.469	0.501-0.610	34.071-40.857
Mean	0.533	0.811	0.406	0.563	37.656
CV	0.107	0.046	0.085	0.055	0.063
m6					
N	13	14	9	8	7
Range	0.381-0.555	0.651-0.826	0.288-0.424	0.402-0.630	31-920-37.643
Mean	0.480	0.749	0.347	0.522	34.239
CV	0.101	0.072	0.117	0.134	0.059
m7					
N	2	2	0	0	0
Range	0.383-0.410	0.484-0.487	–	–	–
Mean	0.396	0.485	–	–	–
CV	0.048	0.004	–	–	–

distinctive molars, identified as m1, have a low, anteriorly placed paraconid, somewhat lower crown in general, low crown width to length ratio, and wide trigonid angle (greater than 60°). The second and third lower molars are progressively shorter, wider, and taller crowned, with a more acute trigonid angle (Table 1; Figs 4-5) and bases of paraconid and metaconid more closely approximated; differences in means for dimensions of m2 and m3 are significant at the $p = 0.05$ level, whereas that for the trigonid angle is not (Table 2). These trends are continued through the fourth molar; the differences in width and length are not significant between m3 and m4, whereas that for the trigonid angle is: m4 has a much more acute angle (Tables 1, 2). The fifth lower molar is nearly as tall as m4, but tooth length and width decrease past m4, and the differences between means are highly significant. Values for trigonid angle overlap considera-

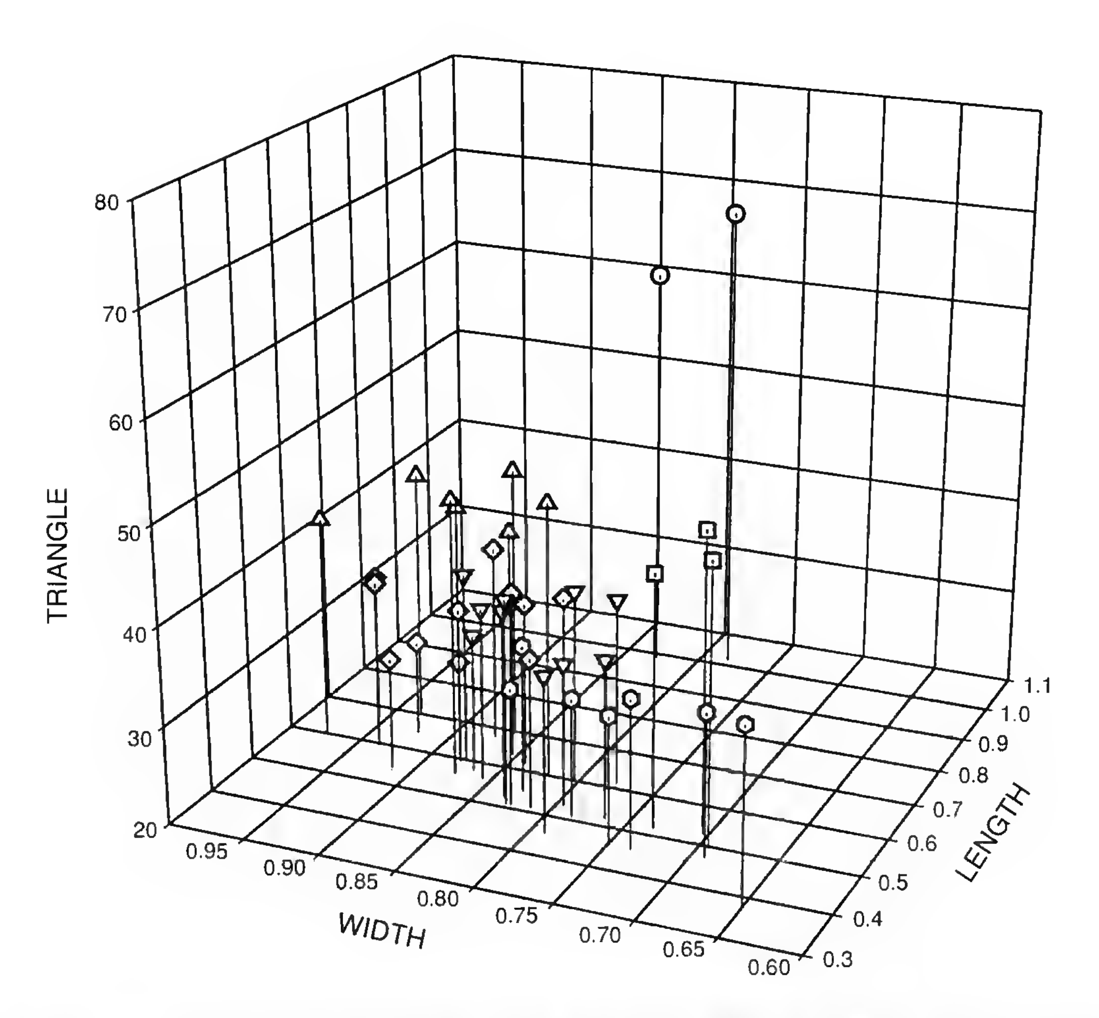


FIG. 5. — Proportional differences (length, width, trigonid angle) according to tooth locus for lower molars of *Spalacolestes cretulablatta*, n. gen., n. sp. Symbols: **circles**, m1; **squares**, m2; **upward pointing triangles**, m3; **diamonds**, m4; **downward pointing triangles**, m5; **hexagons**, m6 (m7 is omitted because it lacks a metaconid and the trigonid angle cannot be calculated).

bly between m4-6 (see comments above), and no consistent pattern is recognizable. On posterior molars, there is a tendency for the paracristid to be slightly longer than the protocristid, whereas the reverse is true for *Symmetrodontoides*. The sixth lower molar is lower crowned and smaller than m5. The last lower molar, m7, is lower crowned yet and is by far the smallest in the series. The metaconid on this tooth is lacking from OMNH 29600 (the holotype) and from one isolated, referred specimen. We consider it unlikely that presence of the cusp is variable within the species, given the distinctiveness of m7, although it is curious that so few molars assignable to this locus were recovered, in view of the large samples of more mesial teeth. The lack of a functional postvallid surface on m7 suggests that, as in *Zhangheotherium* (see Hu *et al.* 1997), *Spalacolestes cretulablatta* had one fewer molar in the upper than lower series. Changes in proportions and trigonid angle through the molar series are summarized in Figure 5, and a composite restoration is shown in Figure 6C, D.

All lower molars are double-rooted. None of the isolated teeth preserves both roots intact, but comparison within this sample, together with preserved alveoli on the jaw fragments assigned to *Spalacolestes cretulablatta*, indicates that the

TABLE 2. — Two-sample *t* test (independent *t* test) comparing mean measurements for adjacent lower molars, *Spalacolestes cretulablatta* n. gen., n. sp. First and last molars omitted because of insufficient data (N for samples are given in Table 1).

	Length	Width	Pad-med	Prd-med	Angle
m2 vs. m3					
Difference between means	0.111	0.157	0.035	0.114	2.213
Pooled variance *t*	- 3.514	- 5.664	- 1.111	- 3.228	1.371
Degrees of freedom	9	12	9	9	8
Probability	0.007	0.000	0.295	0.005	0.208
m3 vs. m4					
Difference between means	0.024	0.011	0.060	0.035	10.882
Pooled variance *t*	0.911	0.437	2.935	-1.460	7.568
Degrees of freedom	20	24	17	18	16
Probability	0.080	0.061	0.009	0.016	0.000
m4 vs. m5					
Difference between means	0.068	0.057	0.007	0.035	2.588
Pooled variance *t*	3.195	3.238	0.487	2.135	-2.041
Degrees of freedom	30	33	21	24	19
Probability	0.003	0.003	0.631	0.043	0.055
m5 vs. m6					
Difference between means	0.053	0.062	0.058	0.041	3.418
Pooled variance *t*	2.685	3.899	3.554	1.887	3.097
Degrees of freedom	29	31	19	20	15
Probability	0.012	0.000	0.002	0.074	0.007

roots were subequal in size (except for m7, in which the distal root is smaller) and mesiodistally compressed, with a characteristic subrectangular cross section that makes edentulous spalacolestine mandibles easily recognized as such. The cingulum is complete on all lower molars and is especially strong on the lingual side of m1 (Fig. 7A, B), where it shows almost no flexure; on subsequent molars, it flexes dorsally between the bases of paraconid and metaconid. The cingulum descends considerably as it extends past the interstitial regions of the tooth, so that the labial part of the crown is much higher than the lingual side. Mesiolingual and distolingual cuspules are present on the cingulum, as they are in other North American Spalacotheriidae; these are variable but are generally salient, projecting somewhat mesially and distally (as well as dorsally) from the cingulum. The paraconid and metaconid of m1 (Fig. 7A, B) have conical, well-separated bases when viewed lingually; the metaconid is about two-thirds the height of the protoconid, whereas the paraconid is less than one-half the height of that cusp when the tooth is viewed lingually. On m2 (Fig. 7C, D), the trigonid angle is more acute, and the bases of paraconid and metaconid are more closely approximated because the former cusp is more posteriorly placed. The paraconid is relatively taller than on m1, but lower than on succeeding molars. The metaconid of m2 is more slender, with a less robust base, than on m1. The lingual cingulum develops a pronounced lingual flexure on m3 (Fig. 7E, F), and this continues on succeeding molars. The labial face of the protoconid on this and succeeding teeth is less rounded and more sharply folded than on m1-2; the metaconid is nearly as tall as the protoconid, with the paraconid being only about half as tall as the protoconid, viewed lingually. Of the two basal cuspules, the distal (i.e., talonid) tends to be the more prominent and projecting; the succeeding tooth fits into the concavity of the distal cingulum formed labial to the distal cingular cusp (see Fox 1976). By m4 (Figs 7G, H, 8, 9), the bases of paraconid and metaconid are appressed, with a more slender, anteroposteriorly compressed appearance than on anterior teeth, when viewed

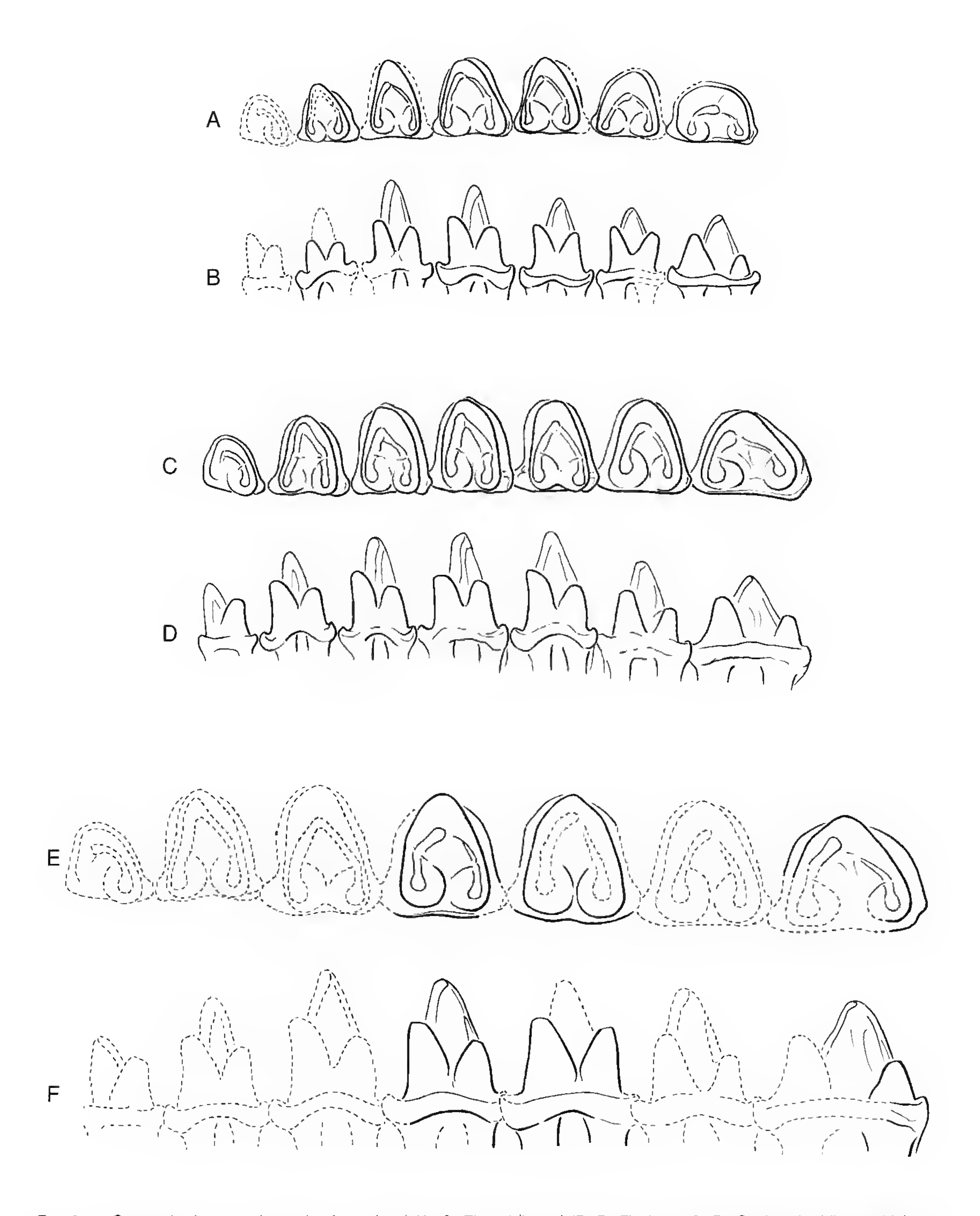


Fig. 6. — Composite lower molar series in occlusal (A, C, E) and lingual (B, D, F) views; **A**, **B**, *Spalacotheridium noblei* n. sp.; **C**, **D**, *Spalacolestes cretulablatta* n. gen., n. sp.; **E**, **F**, *Spalacolestes inconcinnus* n. gen., n. sp. Tooth series scaled to relative size.

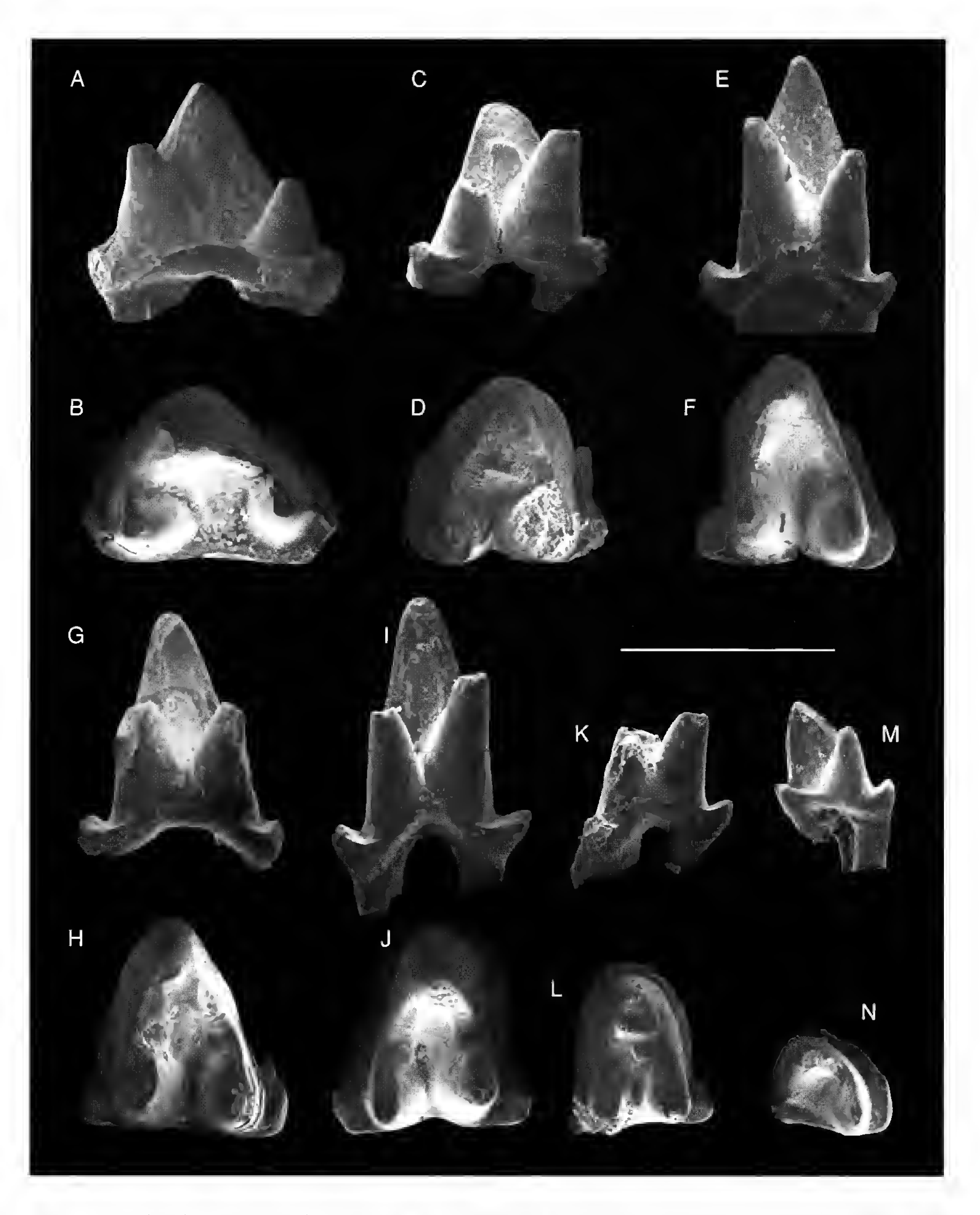


FIG. 7. — Scanning electron micrographs, lower molars of *Spalacolestes cretulablatta* n. gen., n. sp.; A, C, E, G, I, K, M, lingual views; B, D, F, H, J, L, N, occlusal views; **A**, **B**, left m1 (OMNH 26424); **C**, **D**, right m2 (OMNH 33226); **E**, **F**, left m3 (OMNH 33851); **G**, **H**, left m4 (OMNH 26422); **I**, **J**, right m5 (OMNH 30631); **K**, **L**, right m6 (OMNH 27557); **M**, **N**, left m7 (OMNH 27463). Jaw fragments and roots eliminated where needed to improve clarity. Scale bar: 1 mm.

lingually. Lower molars 5 and 6 (Figs 7I-L, 8) are similar, but progressively smaller, with crown height decreasing after an apparent maximum at m4-5. The last lower molar (Figs 7M, N, 8) is distinctive in its much smaller size; although it is two-rooted like more anterior teeth, the metaconid and protocristid are lacking, and the distal cingulum is expanded. The posteriormost molar (m7) of *Spalacotherium* is also quite small, but it retains a full complement of trigonid cusps (see Clemens 1963).

The available series of lower molars of *Spalacolestes cretulablatta* encompasses a wide variety of wear stages. As wear progresses, the V-shaped notches in paracristid and protocristid become rounded and U-shaped. On m1, wear is heaviest on the protocristid, which develops a facet that dips distally. The wear facets on paracristid and protocristid are rather oblique to the occlusal plane in early wear, progressively becoming more parallel to that plane. In advanced wear stages (e.g., OMNH 27569, m6), the crown forms a continuous, concave, triangular wear surface that dips slightly in a mesial direction. Obliquely oriented striations are present on prevallid and postvallid faces of worn molars; these are more pronounced and recognizable on m4-6, where the mesial and distal faces of the teeth are somewhat more planar than on more anterior molars, where they are more convex. The rim of the cingulum forms a sharp ridge in unworn teeth, especially mesially and distally. With wear, small interstitial facets develop mesially and distally, and the sharp mesial and distal rims are beveled off into rather flat, obliquely oriented facets.

Mandible

Aside from small fragments, the dentary of *Spalacolestes cretulablatta* is known from two specimens, OMNH 29600 and 27421 (Figs 8, 9). OMNH 27421 preserves the horizontal ramus ventral to the level of m1, the posterior alveolus of m2, the base of m3, m4-5 intact, and paired alveoli for m6-7. Most of the ascending ramus and angular region are missing. OMNH 29600 (the holotype) includes the horizontal ramus posterior to m3 and preserves m4-7 in place. The crown of m4 is broken from its base and is rotated and displaced; minor postmortem rotation and displacement of the other molars has also occurred. The posterior and inferior margins of the angular region are intact, except for the loss of the condyle. The posterior margin is intact for a short distance dorsal to the position of the condyle; the coronoid process is broken obliquely and its full extent cannot be determined.

The horizontal ramus (Figs 8, 9) has a very gracile appearance compared to that of *Spalacotherium*. The ventral margin of the horizontal ramus appears somewhat bowed in lateral view, owing to a slightly greater depth beneath m4-5 than anteriorly or posteriorly. In dorsal view (Figs 8B, 9B), the ramus is relatively straight posterior to the level of m3; anterior to that tooth position, it curves medially. The ascending ramus arises about a molar's length posterior to the position of m7 and angles dorsally at about 45° with respect to the alveolar margin of the horizontal ramus. The posterior part of the jaw is also remarkably gracile in appearance, the bone being very thin in comparison to the far more robust (and larger) mandible of *Spalacotherium*. Proportionately, the ascending ramus is much longer anteroposteriorly than it is in *Spalacotherium*.

On the lateral side of the jaw (Figs 8C, 9C), the masseteric fossa is well marked and, owing to the form of the angular region (see below) and lateral flexure of the anterior margin of the ascending ramus, has the appearance of being quite deep. There is no labial mandibular foramen present at the apex of the masseteric fossa, as there is in a number of other primitive mammals (e.g., Dashzeveg & Kielan-Jaworowska 1984; Marshall & Kielan-Jaworowska 1992; Cifelli *et al.* 1998), although there is an extremely small nutritive foramen in one specimen (OMNH 29600) at a point somewhat dorsal to the apex of the masseteric fossa.

The anterior margins of the ascending ramus and masseteric fossa flex strongly in a lateral direction as they rise above the alveolar margin of the jaw. Similarly, the inferior margin of the dentary in the angular region has a salient lateral deflection. This strongly deflected angular region and lateral flexure of the anterior margin of the ascending ramus, together with similarly strong features on the lingual side of the mandible, give the dorsal

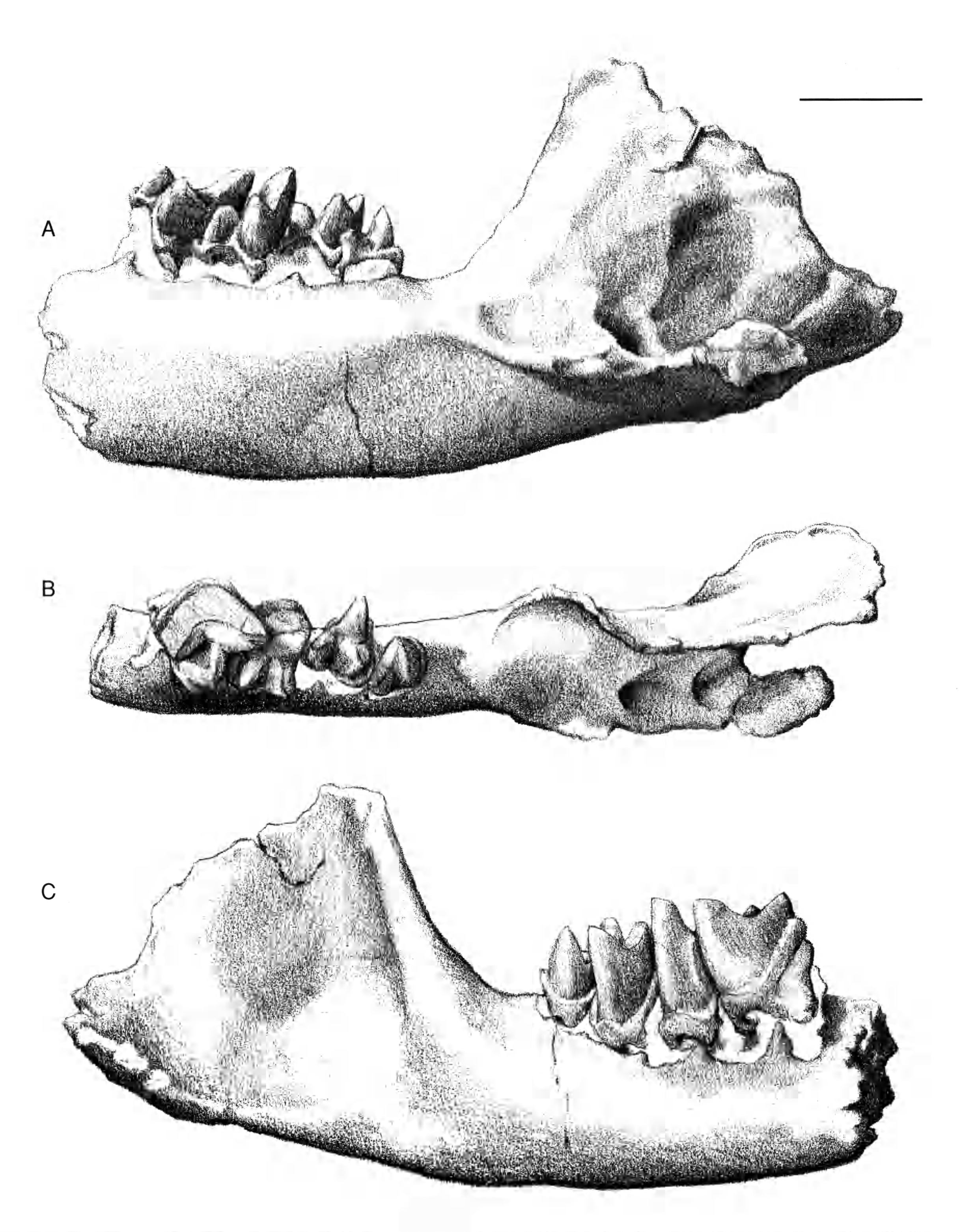


FIG. 8. — Dentary of *Spalacolestes cretulablatta* n. gen., n. sp. holotype (OMNH 29600), right dentary with m4-7, in lingual (**A**), occlusal (**B**), and labial (**C**) views. Scale bar: 2 mm.

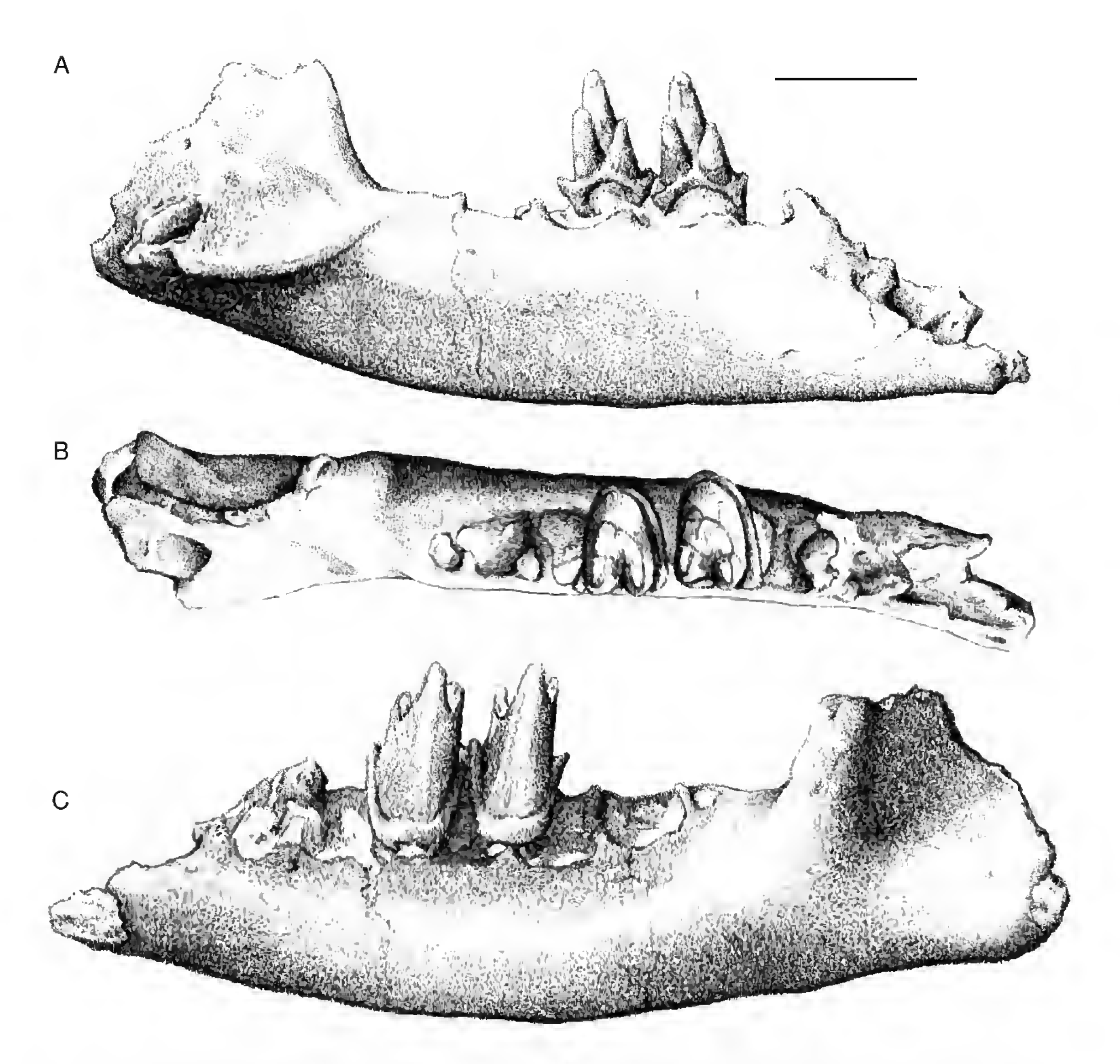


Fig. 9. — Dentary of *Spalacolestes cretulablatta* n. gen., n. sp. (OMNH 27421), left dentary with m4-5, in lingual (**A**), occlusal (**B**), and labial (**C**) views. Scale bar, 2 mm.

(Figs 8B, 9B) and posterior views of the mandible in *Spalacolestes cretulablatta* an appearance that is unique, so far as we are aware, among Mesozoic mammals.

On the lingual side of the jaw (Figs 8A, 9A), a strong crest, which we interpret as being for the insertion of the m. pterygoideus medialis, descends posteroinferiorly from the junction of the horizontal and ascending rami, beginning just below the alveolar margin. This crest strengthens to a shelf as it passes just inferior to the mandibular foramen, which has double openings for the mandibular canal on one specimen (Fig. 8B). The mandibular foramen is comparatively large and faces posterolabially, owing to the great development of the pterygoid crest beneath, the anterior and posterior margins of the mandibular foramen are developed as lips that project lingually as they descend to the pterygoid crest. A short distance posterior to the mandibular foramen, the pterygoid crest is developed as a salient process that thickens into a robust tip. A deep

TABLE 3. — Measurements (mm) and descriptive statistics for upper molars of *Spalacolestes cretulablatta* n. gen., n. sp. See Figure 2 for measurement definitions.

	M1	M2	M3	M4	M5	M6
L (N)	–	2	1	4	1	3
L (Range)	–	1.164-1.225	0.747	0.669-0.846	0.684	0.546-0.552
L (Mean)	–	1.195	0.747	0.745	0.684	0.549
L (CV)	–	0.036	1.000	0.103	1.000	0.006
ANW (N)	1	2	1	5	1	3
ANW (Range)	1.084	0.971-0.988	0.949	0.942-1.113	0.745	0.614-0.682
ANW (Mean)	1.084	0.979	0.949	1.034	0.745	0.656
ANW (CV)	1.000	0.012	1.000	0.065	1.000	0.056
POW (N)	–	3	2	5	1	3
POW (Range)	–	1.152-1.168	1.028-1.038	0.871-1.090	0.962	0.757-0.888
POW (Mean)	–	1.160	1.033	0.994	0.962	0.813
POW (CV)	–	0.007	0.007	0.107	1.000	0.083

pocket is enclosed between the pterygoid process (lingually) and the body of the dentary (labially). Where present, the pterygoid crest commonly extends posteriorly to the condylar region in Mesozoic mammals (e.g., Triconodontidae, Tinodontidae, Dryolestidae, see Simpson 1928a, 1929): in *Spalacolestes cretulablatta*, it terminates at the posterior margin of the process. The pterygoid fossa is very broadly developed anterior to the mandibular foramen, and in this respect differs from that of *Zhangheotherium*.

No meckelian groove or postdentary trough are apparent, nor are seats for the coronoid or other postdentary bones, as commonly seen in primitive mammals (Kermack & Mussett 1958; Kermack *et al.* 1968; Dashzeveg & Kielan-Jaworowska 1984; Kielan-Jaworowska & Dashzeveg 1989; Krebs 1991; Lillegraven & Krusat 1991; Nessov *et al.* 1994). A vestigial trace of the meckelian groove is present anteriorly on the dentary of *Zhangheotherium*, but a postdentary trough is lacking. The condyle is not preserved, but its position is shown by a slight thickening of bone just ventral to the preserved posterior margin of the ascending ramus in OMNH 29600 (Fig. 8A, C). The condyle would have been situated at, or slightly below, the alveolar margin of the horizontal ramus, lower than in *Spalacotherium* (e.g., BM 47750).

Upper molar series

The upper molars (Figs 10, 11) are two-rooted. They lack a lingual cingulum (although a faint basal swelling is variably present), as seen in *Symmetrodontoides canadensis* (see Fox 1985), and cusps on the pre- and postparacrista, as seen on upper molars of *Spalacotherium* (see Simpson 1928a), *Spalacotheroides* (see Patterson 1956), and *Zhangheotherium* (see Hu *et al.* 1997). Acuteness, transverse width, and height of the preparacrista relative to the postparacrista increase from M1 to M4, which is almost completely symmetrical. The parastylar lobe and distal stylar cusp are prominent on anterior molars (as they are in *Symmetrodontoides*), and decrease throughout the series. By contrast, the parastylar lobe is more strongly developed on posterior upper molars of *Spalacotherium* (see, e.g., Clemens 1963). The paracone is most distally recumbent on M1, decreasing in recumbency through M4, where it is symmetrical and erect. Past M4, molars are progressively smaller (Table 3), narrower labiolingually, and have a more posteriorly placed paracone. A composite restoration is shown in Figure 11; many of the trends evident in the restored series are also seen in the composite of *Kuehneotherium* (see Mills 1984).

The distolabial part of M1 (Fig. 10A, B) is not preserved on available specimens. The paracone is strongly recumbent distally; its mesial face is rounded, lacking the "pinched" appearance, with relatively straight shearing surface, of more distal teeth. A weak ridge, which develops heavy wear on its occlusal surface, descends almost vertically from the apex of the paracone down its mesolabial surface; this is equivalent to the prepara-

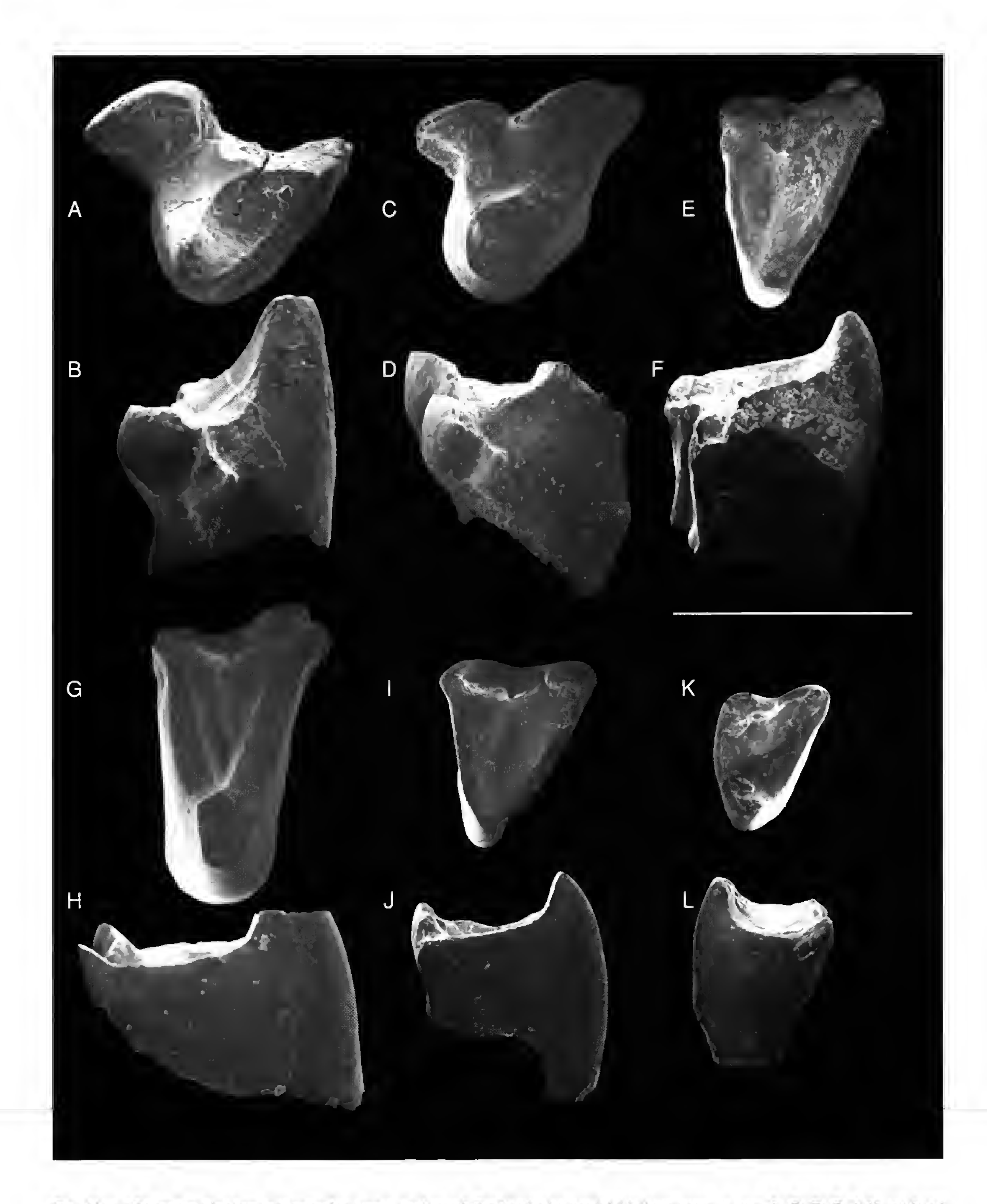


FIG. 10. — Scanning electron micrographs, upper molars of *Spalacolestes cretulablatta* n. gen., n. sp.; A, C, E, G, I, K, occlusal views; B, D, F, H, J, L, mesial views; **A, B**, left M1 (OMNH 26426); **C, D**, left M2 (OMNH 26686); **E, F**, left M3 (OMNH 33060); **G, H**, left M4 (OMNH 30611); **I, J**, left M5 (OMNH 25796); **K, L**, right M6 (OMNH 26691). Jaw fragments and roots eliminated where needed to improve clarity. Scale bar: 1 mm.

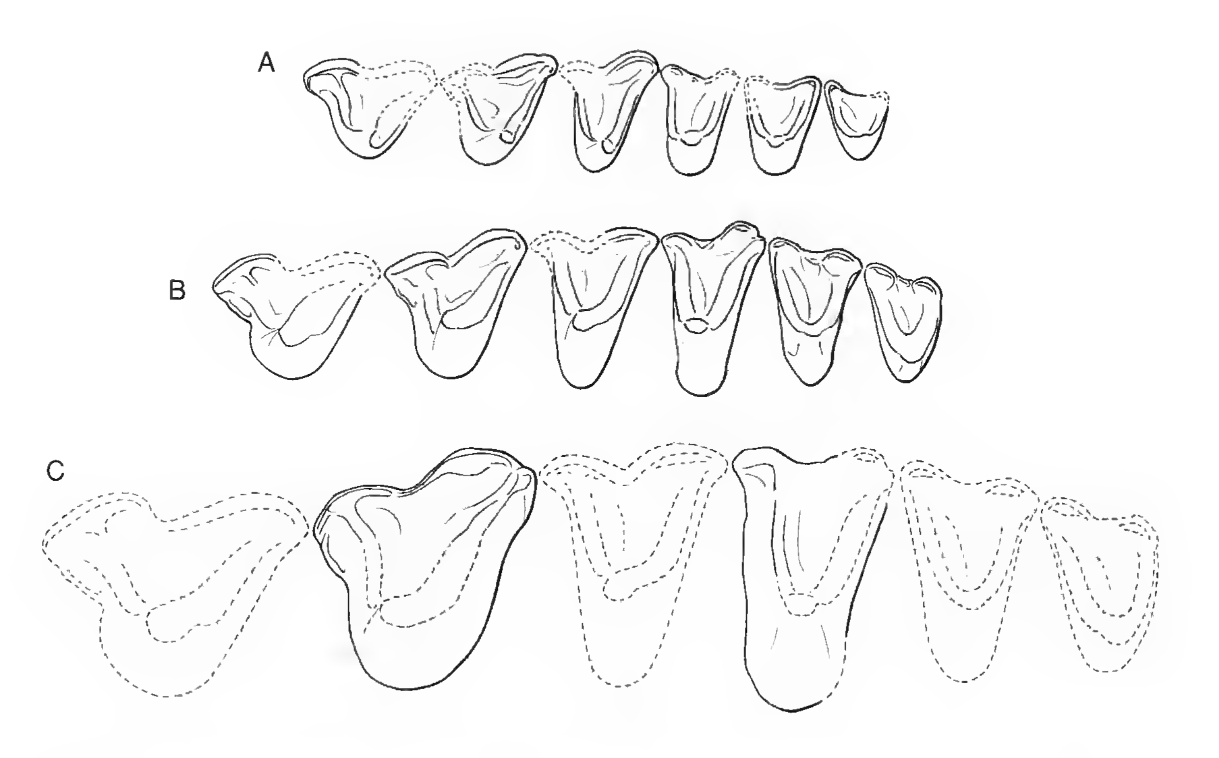


FIG. 11. — Composite upper molar series in occlusal view. **A**, *Spalacotheridium noblei* n. sp.; **B**, *Spalacolestes cretulablatta*, n. gen., n. sp.; **C**, *Spalacolestes inconcinnus*, n. gen., n. sp. Series scaled to relative size.

crista, but a crest as such is not developed until this surface approaches the parastyle, where its presence is only faintly suggested. The parastyle is very low, being placed near the base of the crown, and is developed as a prominent, mesially projecting lobe. A small accessory shelf descends lingually from the parastylar lobe near the labial terminus of the preparacrista, terminating at the base of the crown; there is no other hint of a cingulum, although the enamel is variably swollen on the lingual base of the tooth.

M2 (Fig. 10C, D) is generally similar to that of *Symmetrodontoides*, although the parastyle and metastyle are less developed. It differs from M1 in having a flattened mesial (prevallum) shearing surface, more strongly developed preparacrista, more acute angulation, less recumbency of the paracone, and less prominent, bulbous parastyle. The postparacrista descends at a steep angle from the apex of the paracone, forming a V-shaped notch near the base of that cusp. The crest terminates near the distolabial corner of the tooth, not quite reaching the small metastylar cusp. From the metastyle, a faint crest descends lingually for a short distance along the distal face of the tooth, terminating near the base of the tooth. This crest (perhaps a remnant of a cingulum) evidently formed the margin of the occlusal surface of the tooth, perhaps serving as a guide for the corresponding lower molar shearing surface: it is oriented at the same angle as wear striations located higher and more lingually on the same surface of the molar (e.g., OMNH 32897; Fig. 10C, D). Mesial to and separate from the metastylar cusp is a prominent, mesiodistally elongate, trenchant stylar cusp, as seen in *Symmetrodontoides*. This crestlike cusp extends mesially to the ectoflexus, where it meets a lower crest descending distally from the region of the stylocone. The latter cusp is not preserved on available specimens but, if present, it was small. None of the M3s in the sample is complete, but

available specimens show a continuation of trends established in the upper molar series: the trigon is more acute and deeply basined; the paracone has only slight recumbency; the preparacrista is relatively higher; and the stylar cusp is smaller. One broken specimen (OMNH 33060; Fig. 10E, F) preserves the paraconal crests in pristine condition; cuspules are lacking from these.

M4 (Fig. 10G, H) is the most transversely developed, acute-angled, nearly symmetrical tooth of the series; in *Spalacotherium* (including *Peralestes*), it is M3 that appears to be most nearly symmetrical (Butler 1939). The paracone is mesiodistally compressed, with a distinct lingual fold, and is not recumbent. All specimens are almost perfectly symmetrical, except for minor differences in the parastylar and metastylar regions. The pre- and postparacristae are equal in height, enclosing a rather deep trigon basin, with flat, strap-like facets (as described for *Symmetrodontoides*, see Fox 1976, 1985) on their occlusal surfaces. The labial surface of the tooth bulges adjacent to the labial terminus of the preparacrista, suggesting the presence of a small stylocone (obliterated by wear on available specimens). Mesial to this, the parastyle is much reduced, forming an inconspicuous knob at the mesiolabial corner of the tooth. The metastyle is similarly developed; just mesial to it, the mesiodistally elongate stylar cusp is present along the margin of the stylar shelf. This stylar cusp is variable in development, being largest in the figured specimen (OMNH 30611; Fig. 10G, H), but is much reduced in comparison to more anterior molars. The cusp descends mesially as a crest rimming the stylar shelf and enclosing the trigon basin labially in the region of the ectoflexus, where there is variably (OMNH 26693, 30611) a small cuspule present.

M5 (Fig. 10I, J) is less transverse and forms a more obtuse angle than M4. It is somewhat lower crowned as well, although the pre- and postparacristae are high relative to the apex of the paracone, and enclose a deep trigon basin. The paracone is more distally placed than on M4 or preceding molars, recalling the condition in tribosphenic therians, where the protocone is more distally placed on distal molars. The trend in the molar series toward reduction of the parastyle is complete: no trace of it remains. There is a faint trace of the metastyle at the distolabial corner of the tooth. The distal margin of the stylar shelf is formed by the stylar cusp, which has twinned apices in the single complete specimen (OMNH 25796; Fig. 10I, J). This specimen is virtually unworn, and shows (again) the lack of accessory cusps on the pre- and postparacrista. It also shows that the stylocone, worn away in most other specimens available, is present and is developed as a trenchant, mesially placed counterpart to the distal stylar cusp.

M6 (Fig. 10K, L) is smaller and less transverse than M5. Parastyle and metastyle are lacking, and the labial part of the tooth is instead occupied by the stylocone and the distal stylar cusp, the latter not quite extending to the distolabial corner of the tooth. The paracone is more posteriorly placed than on M5; the distal face of the tooth is distinctive in being curved, with a rounded distolabial corner that differs from the more angular appearance of preceding molars.

Spalacolestes inconcinnus n. sp.
(Figs 6, 11-13)

Holotype. — Right m4, OMNH 33903.

Hypodigm. — The holotype, and **m1**, OMNH 33039; **m3**, 33897; **M2**, 33034; **M4**, 33911.

Locality and horizon. — OMNH locality V868; upper part of Cedar Mountain Formation; Albian-Cenomanian.

Etymology. — *Inconcinnus* (Latin), awkward, coarse, in reference to the appearance of the teeth when compared to the dainty, elegant morphology generally characterizing smaller species of Spalacotheriidae.

Diagnosis. — The larger of the two species referred to the genus; lower molar cingulum better developed mesiolabially on m1 than in *Spalacolestes cretulablatta*, from which it also differs in having the trigon basin incompletely enclosed at the ectoflexus of posterior upper molars. Larger than *Symmetrodontoides foxi*; approximately similar in size to *S. canadensis*, from which it differs in having proportionately narrower lower molars and other generic characteristics.

Description and comments

Teeth of *S. inconcinnus* n. sp. resemble those of

TABLE 4. — Measurements (mm) of *Spalacolestes inconcinnus* n. gen., n. sp.; see Figure 2 for measurement abbreviations and conventions.

Tooth	L	ANW	POW	Pad-med	Prd-med	Angle
m1	–	1.248	–	–	–	–
m3	0.962	1.270	–	0.667	0.739	43.097
m4	1.050	1.314	–	0.660	0.877	39.444
M2	1.861	1.356	1.601	–	–	–
M4	1.033	1.608	1.564	–	–	–

S. cretulablatta in most characteristics, differing chiefly in their much greater size (Fig. 4) and in features probably related to size (such as cusp robusticity). *S. inconcinnus* is much less common than either *S. cretulablatta* or *Spalacotheridium noblei* n. sp., being represented by only five molars, two from the upper dentition and three from the lower.

The lower molars are so similar to those of *S. cretulablatta* that only a few comments are warranted. The cingulum is more strongly developed than in *S. cretulablatta*, particularly on m1 (Fig. 12A, B). In addition, it appears that, in *S. inconcinnus*, the paraconid is lower relative to the metaconid at corresponding tooth positions. Variability cannot be assessed with the sample in hand, however, and this possible difference has accordingly been omitted from the diagnosis.

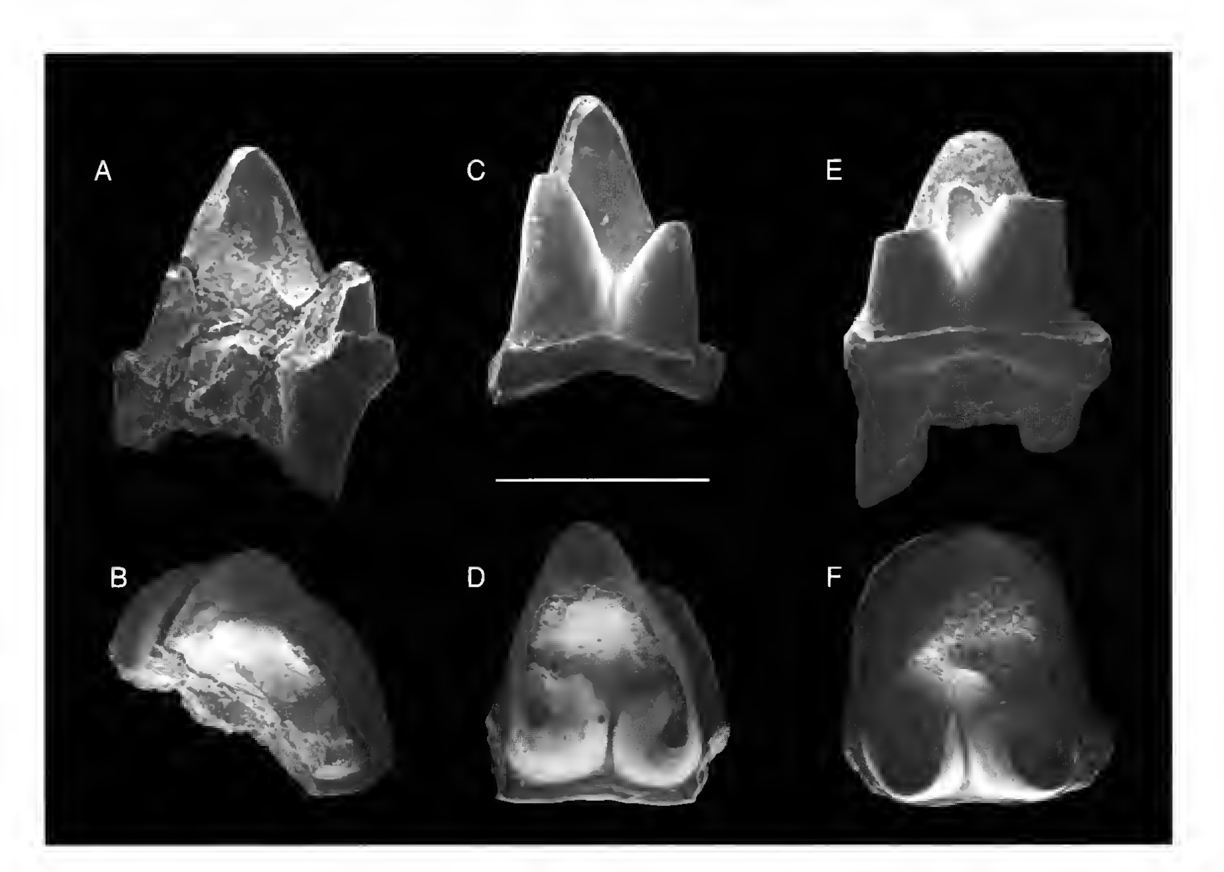


FIG. 12. — Scanning electron micrographs, lower molars of *Spalacolestes inconcinnus* n. gen., n. sp.; A, C, E, lingual views; B, D, F, occlusal views; **A**, **B**, right m1 (OMNH 33039); **C**, **D**, left m3 (OMNH 33897); **E**, **F**, right m4 (holotype, OMNH 33903). Scale bar: 1 mm.

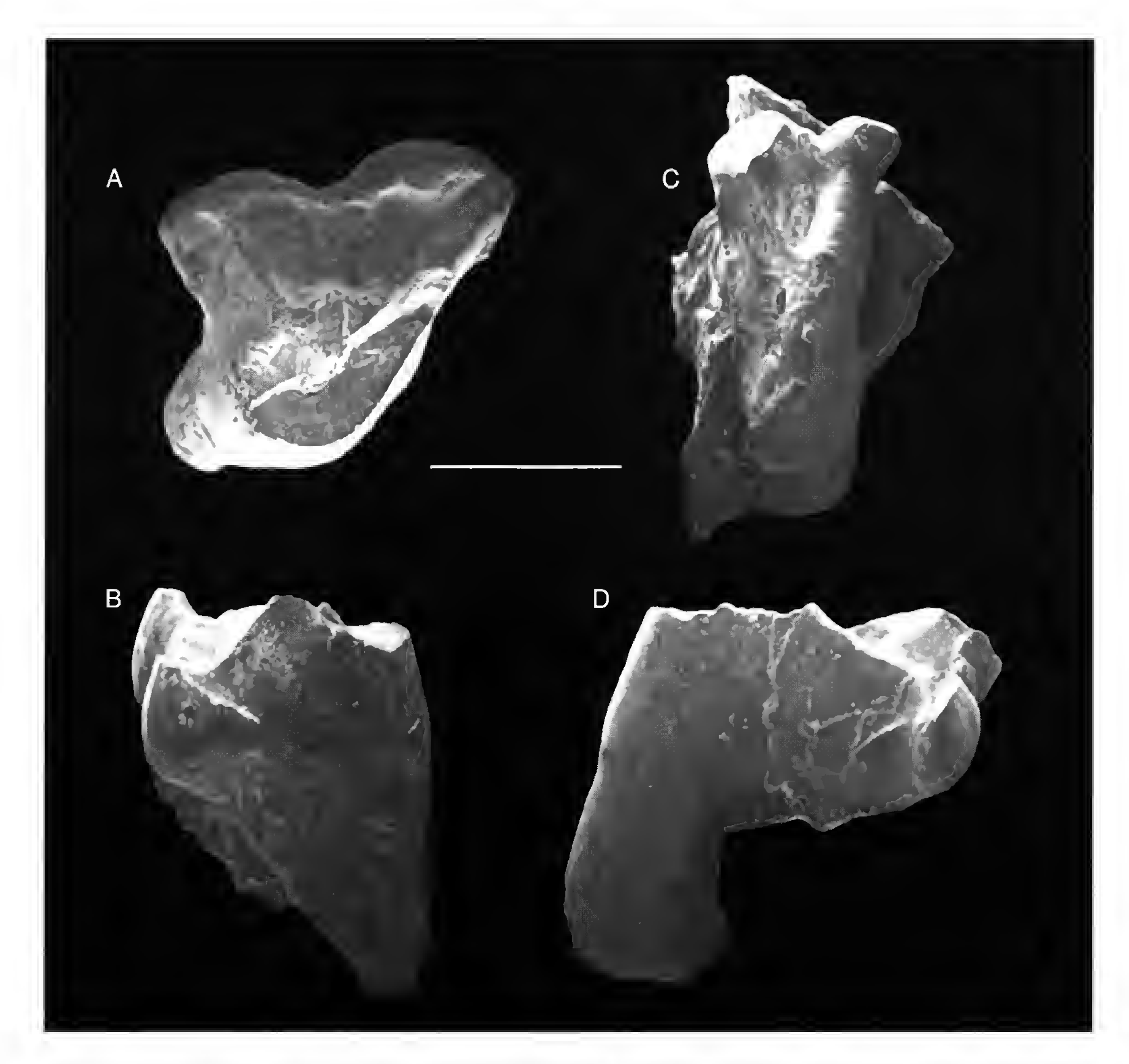


FIG. 13. — Scanning electron micrographs, upper molars of *Spalacolestes inconcinnus* n. gen., n. sp.; A, C, occlusal views; B, D, mesial views; **A**, **B**, left M2 (OMNH 33034); **C**, **D**, right M4 (OMNH 33911). Scale bar: 1 mm.

The only upper molar of *S. inconcinnus* in which the roots can be seen is OMNH 33034 (M2; Fig. 13A, B), where two are present. A faint swelling on the postparacrista, about two-thirds of the distance from paracone to metastyle, suggests the possible presence of a cusp on this crest, but breakage in this region precludes judgment on this point. The crest descending lingually from the metastyle on M2 is stronger but shorter than it is in *S. cretulablatta*. The distal stylar cusp is more bulbous, with a more pronounced labial bulge, than in *S. cretulablatta*; a weak crest, barely hinted at in the latter species, extends lingually into the trigon basin from the base of the stylar cusp. The presence of a small stylocone can be confirmed on M2 of *S. inconcinnus*. On M4 (Fig. 13C, D), the parastylar region and distal stylar cusp are more bulbous than in *S. cretulablatta*, so that the ectoflexus is deeper, although the distal stylar cusp of *S. cretulablatta* variably

projects farther labially than in the single known M4 of *S. inconcinnus*. However, the crests descending to the ectoflexus from the stylocone and distal stylar cusp are very weak, so that the trigon basin is not enclosed labially, as it is in *S. cretulablatta*. OMNH 33911 includes the M4 embedded in a fragment of the maxilla. The labial margin of the tooth is oriented at a high angle with respect to the lateral side of the maxilla (the parastyle is near the lateral margin of the maxilla, whereas the distolabial corner of the tooth is some distance from it), suggesting that the rostrum flared laterally in this region (Fig. 13C).

Genus *Spalacotheridium* Cifelli, 1990

Type species. — *Spalacotheridium mckennai* Cifelli, 1990.

Included species. — The type, and *Spalacotheridium noblei* n. sp.

Distribution. — Albian-Cenomanian through Turonian, Utah.

Revised diagnosis. — Spalacotheriids differing from other members of the family in their small size (maximum length and width measurements of molars generally less than 0.75 mm). Lower molars differ from those of *Spalacotherium* in being more nearly symmetrical and acutely angled; from *Spalacotheroides* in having a complete labial cingulum; and from *Symmetrodontoides* and *Spalacolestes* in being lower crowned, with paraconid and metaconid subequal in development and of approximately equivalent height, only slightly lower than the protoconid, and in having posterior molars that are proportionately narrower and have more obtuse trigonid angles. Upper molars distinct from *Spalacotheroides* in the presence of a larger distally placed stylar cusp and more prominent parastylar hook (anterior loci), the lack of cusps B_1 and C, and the extremely low placement of the preparacrista (anterior loci). Upper molars differ from those of *Spalacolestes* in having a shallower trigon basin, and in the presence of a prominent parastyle on M6.

Comments

This genus was originally based on a single molar of the type and then only species (Cifelli 1990). The recovery of another species, represented by a much more extensive sample from the Cedar Mountain Formation, upholds the morphological distinctiveness of these tiny symmetrodonts. Lower molars of *Spalacotheridium* are generally similar to *Spalacotheroides*, except for the described lack of a labial cingulum in the latter, but available materials of *Spalacotheroides* do not permit comparison between the two. In contrast, the upper molars of the two taxa are quite different. By comparison with *Spalacotherium*, *Spalacotheridium* appears to be primitive with respect to *Symmetrodontoides* and *Spalacolestes* in the features cited in the diagnosis.

Spalacotheridium noblei n. sp.
(Figs 6, 11, 14-16)

Holotype. — OMNH 25828, left m4.

Hypodigm. — The holotype, and the following isolated teeth:
Lower molars: **m1**, OMNH 25609, 33038, 33205, 33221; **m2**, OMNH 30623, 33219; **m3**, OMNH 27261, 29605, 30630, 32948, 33041, 33229, 33900; **m4**, OMNH 25794, 26421, 27424, 27441, 27593, 29766, 30626, 30629, 32946, 33215, 33902; **m5**, 27258, 27629, 29607, 29653, 33052, 33053, 33224, 33899; **m6**, 29602.
Upper molars: **M1**, OMNH 26429; **M2**, OMNH 33061; **M3**, OMNH 30618, 33895; **M4**, OMNH 26689, 26692, 30617, 33232; **M5**, OMNH 27595, 33912; **M6**, OMNH 27461.

Additional referred specimens. — Incomplete upper molars, locus uncertain: OMNH 26687, 33236.

Localities and horizon. — OMNH localities V235, V239, V240, V695, V696, V801, and V868; upper part of Cedar Mountain Formation; Albian-Cenomanian.

Etymology. — For the Samuel Roberts Noble Foundation of Ardmore, Oklahoma, in recognition of its support for the Oklahoma Museum of Natural History.

Diagnosis. — Differs from the most similar species, *S. mckennai*, in having smaller (especially in length) lower molars, with more acute trigonid angle on m4.

Comments and description

S. noblei is rather similar to *S. mckennai* and is distinguishable because the sample of lower molars is sufficient to show that the few known specimens of the latter fall outside the range of size variation in *S. noblei*. The holotype of *S. mckennai* (MNA 5792), identified as m2, has

TABLE 5. — Descriptive statistics for lower molar measurements (mm) of *Spalacotheridium noblei* n. sp. See Figure 2 for measurement abbreviations and conventions.

	L	ANW	Pad-med	Prd-med	Angle
m1					
N	1	4	0	2	0
Range	0.888	0.692-0.722	–	0.532-0.626	–
Mean	0.888	0.710	–	0.579	–
CV	1.000	0.018	–	0.115	–
m2					
N	2	2	2	2	2
Range	0.447-0.482	0.475-0.601	0.359-0.398	0.396-0.441	49.781-54.643
Mean	0.465	0.538	0.379	0.418	52.212
CV	0.053	0.166	0.073	0.076	0.066
m3					
N	6	7	5	7	5
Range	0.421-0.539	0.633-0.795	0.340-0.411	0.416-0.511	42.789-47.581
Mean	0.490	0.711	0.393	0.460	45.490
CV	0.087	0.090	0.076	0.072	0.042
m4					
N	10	12	8	9	8
Range	0.411-0.559	0.559-0.745	0.318-0.389	0.402-0.562	33.018-41.155
Mean	0.485	0.678	0.358	0.490	38.105
CV	0.080	0.073	0.064	0.093	0.075
m5					
N	7	8	2	5	2
Range	0.409-0.465	0.608-0.720	0.348-0.360	0.424-0.492	37.875-39.004
Mean	0.446	0.671	0.354	0.452	38.439
CV	0.043	0.067	0.024	0.055	0.021
m6					
N	1	1	1	1	1
	0.352	0.537	0.270	0.400	36.642

length and width proportions similar to those of m3 in *S. noblei*, which is considerably larger, but the trigonid angle of MNA 5792 is much greater. When compared to m2 of *S. noblei*, on the other hand, MNA 5792 differs greatly in its proportions, falling near the maximum for width and the minimum for length (Tables 5, 6). All molars of *S. noblei* are shorter than m4 of *S. mckennai*, which has a relatively obtuse trigonid angle, despite its tooth position.

The lower molars of *Spalacotheridium noblei* differ from those of *Spalacolestes* and *Symmetrodontoides* in being proportionately lower crowned, with somewhat more obtuse trigonid angles at corresponding tooth positions. The most nearly complete m1 is OMNH 25609, which lacks only the tip of the metaconid and parts of the cingulum adjacent to that cusp (Fig. 14A, B). The paraconid appears to be relatively taller, with a broader, more robust base than is the case in *Symmetrodontoides* or *Spalacolestes*, although it is

TABLE 6. — Upper molar measurements (mm) of *Spalacotheridium noblei* n. sp. See Figure 2 for definition of measurements. Where more than one specimen was measureable a range is given: sample size for each appears in parentheses.

Tooth	L	ANW	POW
M1	–	1.175	–
M2	–	–	0.896
M3	0.646	0.743	0.917-0.957 (2)
M4	0.537-0.551 (3)	0.628-0.827 (2)	0.754-0.838 (3)
M5	0.649	0.795	0.746-0.838 (2)
M6	0.435	0.548	0.441

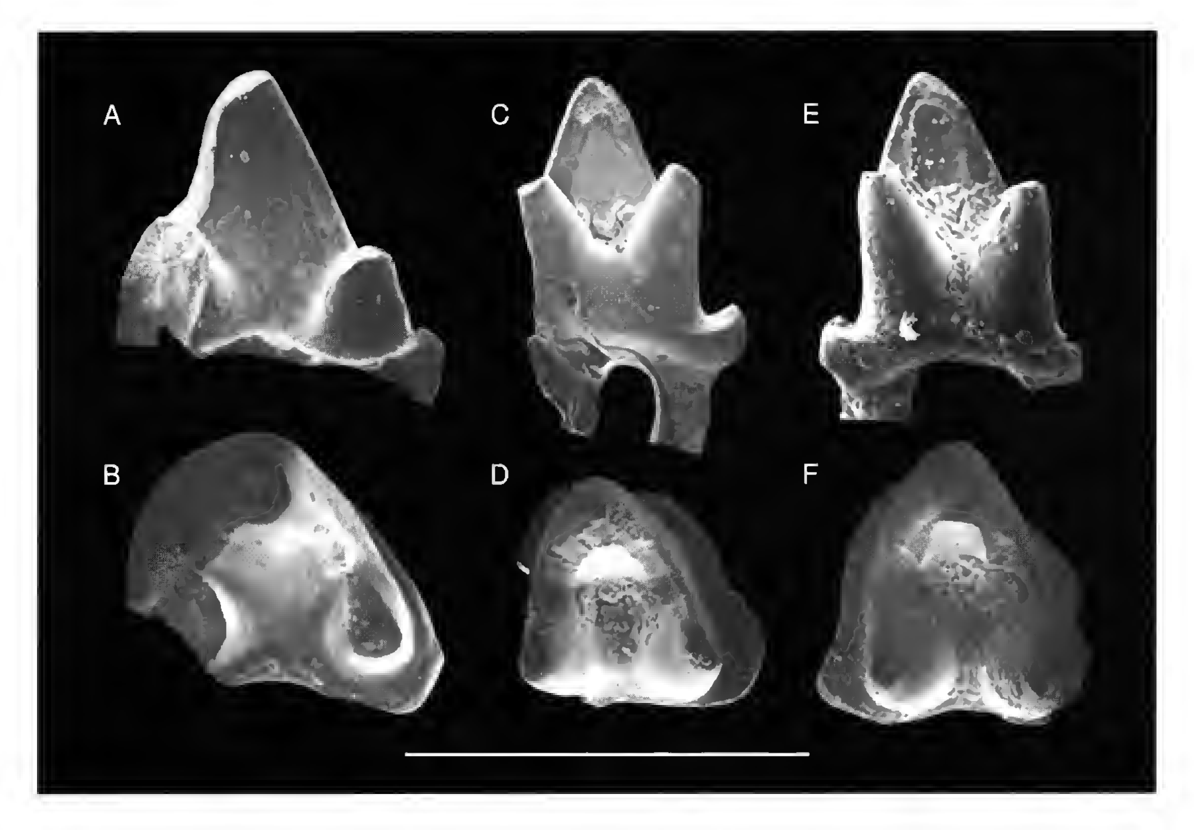


Fig. 14. — Scanning electron micrographs, anterior lower molars of *Spalacotheridium noblei* n. sp.; A, C, E, lingual views; B, D, F, occlusal views; **A, B**, left m1 (OMNH 26429); **C, D**, right m2 (OMNH 33219); **E, F**, left m4 (holotype, OMNH 25828). Scale bar: 1 mm.

still lower than the metaconid. As in all other North American Spalacotheriidae, m1 is morphologically distinctive by virtue of the anterior placement of the paraconid. Length to width proportions appear to change through the molars series about as in *Spalacolestes cretulablatta*, known by a much larger sample; the teeth are lower crowned than in *Symmetrodontoides* or *Spalacolestes*. The second molar (Fig. 14C, D) is considerably shorter than the first; absolute width increases through m4, with m5-6 being sequentially shorter and narrower than m4 (Table 5). On m2 and succeeding teeth, the paraconid is subequal to the metaconid and both cusps are taller relative to the protoconid than in *Spalacolestes* or *Symmetrodontoides*. However, the paracristid dips slightly lower in its median notch than does the protocristid. The cingulum is complete and, as in *Spalacolestes* and *Symmetrodontoides*, bears prominent cuspules at the mesio- and distolingual corners of the tooth. Also as in those taxa, the crown is much taller labially than lingually, and as a result, the cingulum descends noticeably as it proceeds labially from the interstitial regions of the tooth. On m4 (Fig. 14E, F), the metaconid is somewhat more lingually placed than the paraconid, so that the protocristid is slightly longer than the paracristid – a condition reminiscent of what is seen in *Symmetrodontoides*, although not so extreme, and the posterior molars never achieve the remarkable transverse expansion seen in that genus. The dental formula cannot be established with certainty. Identification of OMNH 29602 (Fig. 15C, D) as m6, however, seems probable because of its small size, low crown height, and proportions. This specimen appears to have an interstitial wear facet on the distal cingulum, suggesting the presence of a seventh molar; we tentatively regard the lower series to include seven molars.

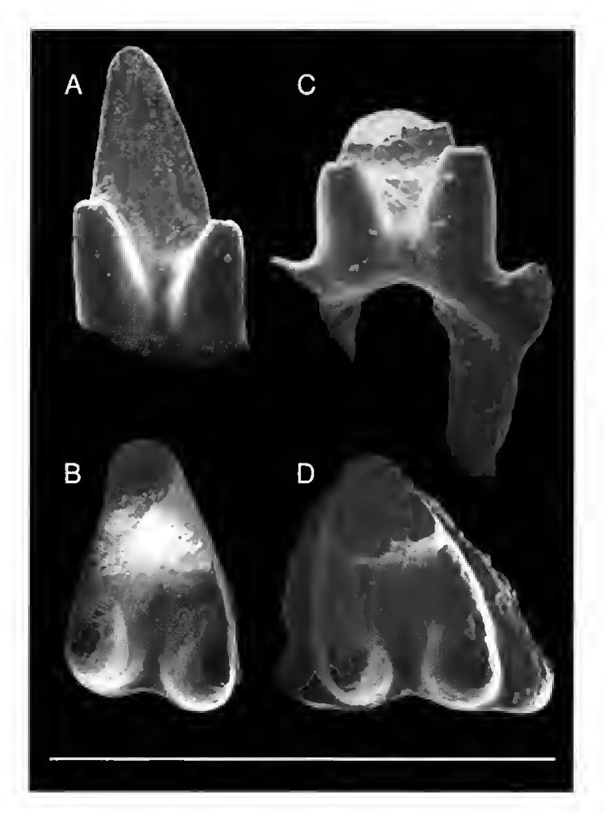


FIG. 15. — Scanning electron micrographs, posterior lower molars of *Spalacotheridium noblei* n. sp.; A, C, lingual views; B, D, occlusal views; **A**, **B**, left m5 (OMNH 27629); **C**, **D**, left m6 (OMNH 29602). Scale bar: 1 mm.

Wear on molar cusps and crests, prevallid and postvallid surfaces, and cingula is similar to that seen in *Symmetrodontoides* and *Spalacolestes* (see Fox 1976; Cifelli & Madsen 1986; and description above, see also Crompton *et al.* 1994 for discussion of the relationship between apical wear, shearing surfaces, and enamel microstructure). Strap-like facets develop along the dorsal surfaces of paracristid (where it develops earliest and most strongly; e.g., OMNH 27424) and protocristid, joining at the protoconid; as wear proceeds, these gradually form a triangular, concave facet with an emarginated base (corresponding to the notch between the bases of paraconid and metaconid). An unusual variant is OMNH 33899, a heavily worn m5 in which wear is stronger on the labial than lingual side of the tooth, with the result that the paraconid and metaconid are taller than the protoconid.

Upper molars (Figs 11, 16) are generally similar to those of *Spalacolestes cretulablatta* and will be described only where they differ or provide additional information. M1 (Fig. 16A, B) is slightly worn, but shows that the stylocone was little developed or absent. The parastylar shelf, which descends lingually from the mesolabial corner of the tooth, has a more planar surface than in *Spalacolestes cretulablatta*. This may be related to differing wear on the available specimens: the parastylar shelf bears a wear facet that is contiguous with the prevallum shearing surface, suggesting that the shelf may have served as a guide for the occluding lower molar. No complete or lightly worn specimens of M2-3 (Fig. 16C) are available; as far as can be determined, they show the progressive narrowing of the paracone and reduction of parastyle and metastyle seen in *S. cretulablatta* (Fig. 11); the metastyle appears to be less developed on corresponding teeth than in that species. The trigon basin is not nearly as deep as in *S. cretulablatta* or *Symmetrodontoides*; this is particularly noticeable on M4-5 (Fig. 16F-I), in which there is little relief on specimens that are only lightly worn (e.g., OMNH 26692, 27595). As with *Spalacolestes* and *Symmetrodontoides*, M4 is the most transversely developed of the upper molars, and is almost perfectly symmetrical. M6 (Fig. 16J) is impressive by virtue of its minuscule size, probably being smaller relative to M5 than in *Spalacolestes*. It is similar in having a curved distal surface and rounded metastylar region, but differs in being less transverse and in having a more prominent, projecting parastyle.

?Spalacotheriidae gen. & sp. indet.
(Fig. 17)

SPECIMENS. — Anterior lower molar, probably m2, OMNH 33896 (OMNH locality V868); posterior upper molar, perhaps M6, OMNH 29612 (OMNH locality V695).

COMMENTS AND DESCRIPTION

Two specimens (one upper molar and one lower molar) from the upper Cedar Mountain Formation cannot be referred to any of the three species described herein, and thus document the presence of at least one more species of non-

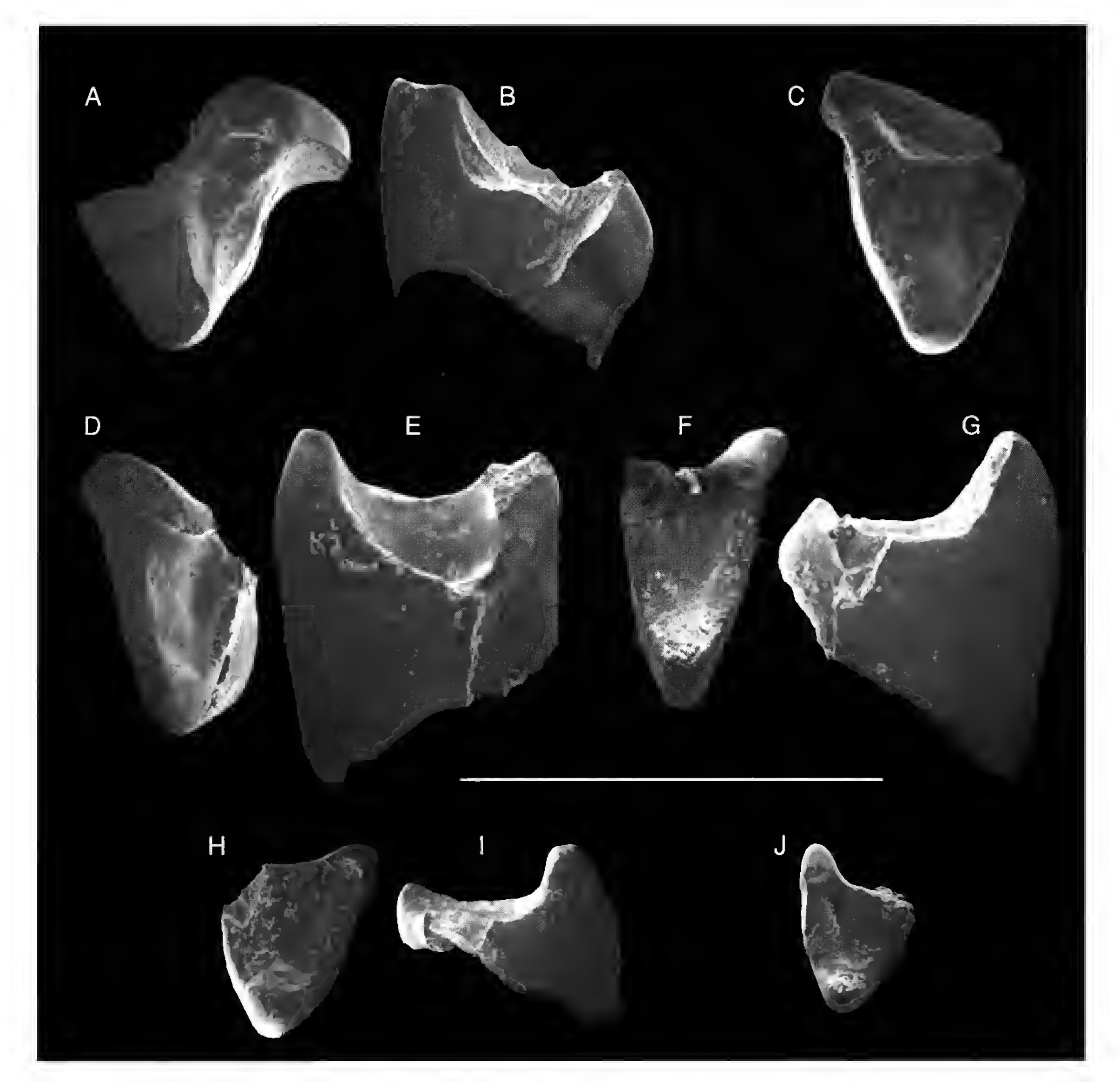


FIG. 16. — Scanning electron micrographs, upper molars of *Spalacotheridium noblei* n. sp.; A, C, D, F, H, J, occlusal views; B, E, G, I, mesial views; **A**, **B**, right M1 (OMNH 26429); **C**, right M2 (OMNH 33061); **D**, **E**, right M3 (OMNH 33895); **F**, **G**, left M4 (OMNH 26692); **H**, **I**, left M5 (OMNH 27595); **J**, left M6 (OMNH 27461). Scale bar: 1 mm.

tribosphenic Theria in the Mussentuchit local fauna. If locus is correctly interpreted, the teeth appear to come from animals of rather different size; hence, they cannot be referred to the same species based on present knowledge.

The lower molar (Fig. 17A, B), tentatively identified as m2, is intermediate between m1 and m2 of *Spalacolestes* or *Spalacotheridium* in terms of length-width proportions and general appearance: the paraconid is somewhat displaced anteriorly and in this respect is reminiscent of a spalacotheriid m1 (although it is not nearly so anteriorly placed as in m1 of all taxa known from the North American Cretaceous), yet this cusp is better developed, the crown is taller, and the trigonid angle more acute than is generally seen on that tooth. These features suggest that it is m2, implying that the specimen may represent a

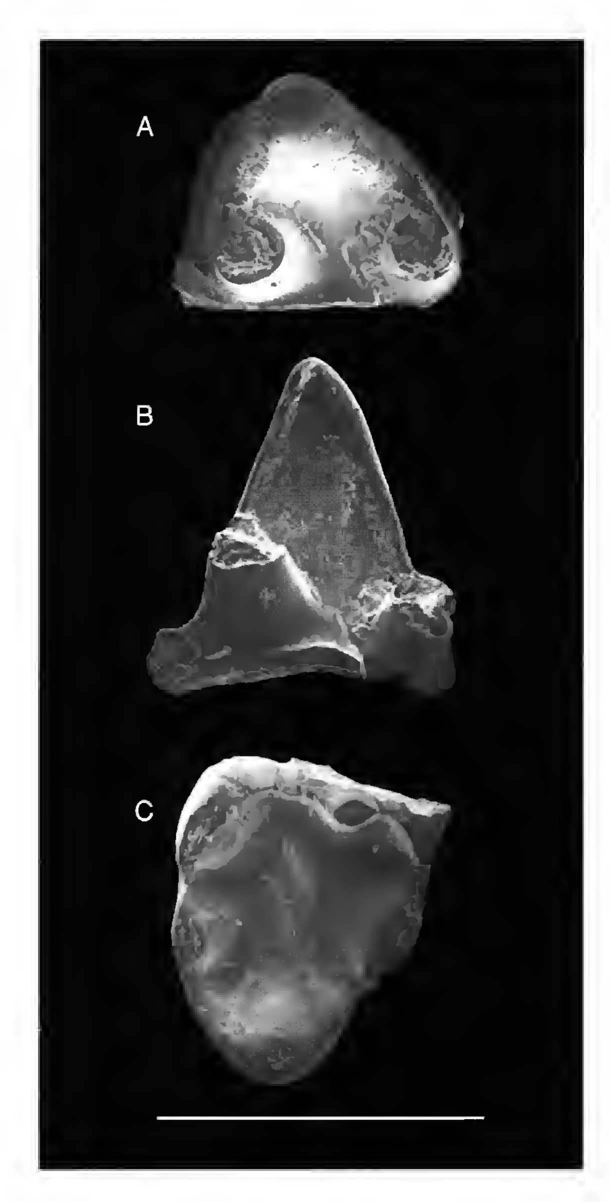


Fig. 17. — Spalacotheriidae gen. and sp. indet., **A**, **B**, left m2? (OMNH 33896) in occlusal (A) and lingual (B) views; **C**, right M6? (OMNH 29612) in occlusal view. Scale bar: 1 mm.

more primitive species than others known from the medial and Late Cretaceous of North America.

The upper molar (OMNH 29612; Fig. 17C) is strongly dissimilar to those of *Symmetrodontoides*, *Spalacotheridium*, and *Spalacolestes*. The absence of a metastylar projection, curvature of the postparacrista and rounding of the metastylar region, mesiodistal breadth and low height of the paracone relative to the rest of the crown, and possible projecting parastylar region (the tooth is broken), suggest that it represents a posterior locus, probably the last (M6, if the dental formula was as hypothesized for *Spalacolestes*). The metastylar cusp is prominent, and there is a second cusp (C) on the postparacrista, about midway between the paracone and the metastylar cusp, and separated from the latter by a slight notch. A weak crest extends into the trigon basin from the base of the paracone. The preparacrista is slightly lower than the postparacrista, and bears a cusp (B_1) that is somewhat closer to the stylocone (which is broken) than the paracone. Distal to the stylocone is a small but trenchant, mesiodistally elongate cusp that rims the labial margin of the trigon basin. A crest extending distally from this cusp does not quite reach the metastylar cusp, leaving the trigon basin open distolabially.

The presence of cusps B_1 and C on the pre- and postparacristae suggests that the upper molar (like the lower) represents a more primitive taxon than named species of Spalacotheriidae from the medial and Late Cretaceous of North America, and are resemblances to taxa such as *Spalacotheroides* (see Patterson 1956, fig. 1), *Zhangheotherium* (see Hu *et al.* 1997, fig. 2), and *Spalacotherium* (see Simpson 1928a, fig. 34); but it clearly differs from upper molars of these as well. Indeed, the presence of a crest extending labially from the paracone is a similarity to dryolestoids. Lacking any reasonable basis for comparison, we defer further comment on these puzzling specimens pending recovery of additional materials.

Genus *Symmetrodontoides* Fox, 1976

Type species. — *Symmetrodontoides canadensis* Fox, 1976.

Included species. — The type, *S. foxi* Cifelli & Madsen, 1986, and *S. oligodontos* Cifelli, 1990.

Distribution. — Turonian through early Campanian, western North America.

Revised diagnosis. — Large spalacotheriids differing from other members of the family in having proportionately broad, acutely-angled posterior lower molars

(m4-6). Differs from *Spalacotheridium* in having lingually placed paraconid and height differential between paraconid and metaconid; differs from *Spalacolestes* in having more pronounced height differential between paraconid and metaconid; differs from both in having taller paraconid on m1, with taller paracristid. M1-2 differ from those of *Spalacolestes* and *Spalacotheridium* in having a paracone with less bulbous base and lingual face tightly arced or folded, not gently curving.

COMMENTS

Symmetrodontoides is not present in the Cedar Mountain Formation; its contents and diagnosis are included herein only to provide a basis for comparison. More extended diagnoses of *Symmetrodontoides* were given by Fox (1976, 1985), based on comparison with *Spalacotherium* and the single lower molar of *Spalacotheroides*. The discovery of additional taxa from the Cretaceous of North America shows that certain features cited in the earlier diagnoses of *Symmetrodontoides*, such as the presence of a labial cingulum and the progressive change in trigonid angle of the lower molars series, have a broader distribution than previously known.

DISCUSSION

Fragmentary as they are, new materials from the Cedar Mountain Formation of Utah add substantially to knowledge of symmetrodont diversity and morphology in the North American Cretaceous. Because many taxa are based on fragmentary, often non-comparable remains; because their teeth (upon which most taxa are based) are of rather simple construction; and because they remain poorly known in general, we do not believe that existing data are sufficient for synthetic consideration of symmetrodont phylogeny in the context of early mammal radiations. Accordingly, we restrict our treatment of relationships to discussion of character distributions and their possible implications for affinities of and within the Spalacotheriidae, summarizing these data in a traditional hypothesis of relationships within the family.

Sigogneau-Russell & Ensom (1998) have presented a detailed treatment of molar characteristics in Symmetrodonta (including many enigmatic taxa not treated herein), and we have relied on their work in compiling the following comparisons. These authors also point out that, in a number of respects, molars of spalacotheriid symmetrodonts are difficult to distinguish from those of certain dryolestoid eupantotheres; indeed, it is possible that dryolestoids are more closely related to spalacotheriids than has been generally believed (see, e.g., Sigogneau-Russell 1991a). In fulfilling our intent to focus on Spalacotheriidae, we cannot attempt comprehensive comparisons herein. We acknowledge the existence of a number of similarities in the molars of advanced spalacotheriids and certain dryolestids, such as the presence of a distal stylar cusp and a hooklike parastylar lobe, mesodistal compression of the crown, and other features cited by Sigogneau-Russell & Ensom (1998), as well as the markedly lower placement of lower molar labial cingulum than lingual cingulum. At the present state of knowledge, we believe that referral of the taxa considered herein from the North American Cretaceous (*Spalacotheroides, Symmetrodontoides, Spalacotheridium, Spalacolestes*) to Spalacotheriidae is more compelling than to Dryolestidae, based on features of the dentary (e.g., peculiar development of the pterygoid crest and masseteric flange) and lower dentition (e.g., extreme reduction of the talonid and characteristics of the roots, see Butler 1939). Based on size, morphological appropriateness and dissimilarity to other known elements of the Mussentuchit local fauna, and (especially) relative abundance and distribution among the known localities, we believe there is vanishingly little doubt as to the reference of upper and lower dentitions to the respective species described herein.

DENTARY

The structure of the dentary and associated postdentary bones has figured prominently in discussion of the origin and early differentiation of mammals (e.g., Crompton & Jenkins 1979; Kemp 1983). Mandibles ascribed to *Kuehneotherium* suggest that a full complement of attached postdentary bones was retained (Kermack *et al.* 1968), as they were in *Morganucodon* (see

Kermack *et al.* 1973), *Docodon* Marsh, 1881 (see Kermack & Mussett 1958), and *Haldanodon* Kühne & Krusat, 1972 (see Lillegraven & Krusat 1991). In these taxa, the posteromedial face of the dentary bears a prominent postdentary trough, overhung by a ridge, extending anteriorly from the condyle. The postdentary trough housed the articular, prearticular, surangular, and angular; attachment facets for the coronoid and splenial are generally also visible, more anteriorly on the dentary (e.g., Kermack *et al.* 1973, fig. 7; Lillegraven & Krusat 1991, fig. 14). The meckelian groove extends anteriorly from the mandibular foramen and is confluent with the postdentary trough; in *Morganucodon* it housed the anterior part of the prearticular (Kermack *et al.* 1973), whereas a splenial is associated with (or overlies part of) the meckelian groove in *Haldanodon* (see Lillegraven & Krusat 1991). Several other poorly understood or archaic mammals retain an essentially similar condition, although the trough and ridge are not as well developed (e.g., *Shuotherium* Chow & Rich, 1982; *Ausktribosphenos* Rich *et al.*, 1997). In most remaining mammals, the meckelian groove (where present) is separated from the mandibular foramen and the postdentary trough and corresponding ridge are lost, suggesting detachment of the main body of postdentary elements from the dentary, although attachment at their anterior extremity evidently persisted in some eupantotheres, such as *Amphitherium* Blainville, 1838 and *Peramus* Owen, 1871 (see Allin & Hopson 1992). The condition may be similar in the Late Jurassic or Early Cretaceous symmetrodont *Zhangheotherium*, which has a prominent meckelian groove and scars for the coronoid and splenial (Hu *et al.* 1997), and, possibly, another element in addition to the dentary (R. C. Fox, pers. comm.). A small coronoid apparently persisted in numerous mammalian groups. First reported among "pantotheres" by Krebs (1969), facets suggesting presence of the coronoid have been reported in the dryolestoid *Henkelotherium* Krebs, 1991 (see Krebs 1991), various triconodonts including *Phascolotherium* Owen, 1838 (BM 112) and *Gobiconodon* Trofimov, 1978 (see Jenkins & Schaff 1988), the eutherian *Prokennalestes* Kielan-Jaworowska & Dashzeveg, 1989 (see Kielan-Jaworowska & Dashzeveg 1989), paulchoffatiid multituberculates (Hahn 1977), and the spalacotheriid *Spalacotherium* (BM 47750). Persistence of the meckelian groove (or a remnant of it), which may have housed remnants of one or more postdentary elements, is even more widespread (see discussions in Bensley 1902; Simpson 1928b; Kermack *et al.* 1973). Among symmetrodonts, the meckelian groove is present in *Kuehneotherium* (see Kermack *et al.* 1968), *Tinodon* (see Simpson 1929), *Zhangheotherium* (see Hu *et al.* 1997), *Shuotherium* (see Chow & Rich 1982), and *Spalacotherium* (see Simpson 1928a). The presence and form of the meckelian groove have been used in interpreting the phylogeny of Mesozoic mammals (Luo 1994; see also Hu *et al.* 1998). Among the aforementioned taxa, the meckelian groove is reduced anteriorly in all; in *Zhangheotherium*, what remains is subparallel to the axis of the dentary, whereas in *Kuehneotherium*, *Tinodon*, *Spalacotherium*, *Tinodon*, and *Shuotherium* the meckelian groove converges toward the ventral margin of the dentary anteriorly. This latter state is presumed to be more derived (Luo 1994), but the significance of this distribution for symmetrodonts is unclear. Both the coronoid and meckelian groove are lacking in *Spalacolestes*, and available evidence suggests that the meckelian groove, at least, was lacking in *Symmetrodontoides*. Hence, both of these features were lost within Spalacotheriidae, assuming monophyly of the family.

In primitive mammals such as morganucodontids and *Kuehneotherium*, the ventral margin of the dentary is emarginated posteriorly (as it is in advanced cynodonts), where the postdentary elements are positioned (see, e.g., Kermack *et al.* 1968, 1973; Gambarayan & Kielan-Jaworowska 1995). The evolution of an angular region and process on the dentary of more derived mammals is uncertain because of disputed homologies and differing criteria on which recognition of these characters are based (see excellent discussion in Wible 1991). An anteriorly placed process is present in cynodonts (Sues 1986) and certain primitive mammals, such as *Morganucodon* (see Kermack *et al.* 1973), *Docodon* (see Kermack & Mussett 1958), and *Haldanodon* (see Lillegraven

& Krusat 1991). Rowe (1988) considered the loss of the anteriorly placed process as an advanced feature characterizing multituberculates and therians. Patterson (1956) disagreed with identification of this feature as a true angular process, pointing out the differences in both position and inferred function (see also Prothero 1981). In *Dinnetherium* Jenkins *et al.*, 1983 (see Jenkins *et al.* 1983), this anteriorly placed process occurs together with one that is more posteriorly placed, near the condyle, supporting Patterson (1956)'s suggestion that the former is not homologous with the angular process found among therian mammals (Jenkins *et al.* 1983; see also Crompton & Luo 1993). Sues (1986; see also Gambarayan & Kielan-Jaworowska 1995), however, suggested that the angular process of tritylodont therapsids and certain therians is homologous, indicating that the continuous ventral margin of the dentary as seen in taxa such as symmetrodonts could have been formed through fusion of the two processes seen in *Dinnetherium*. We can offer nothing in the way of new data to resolve this issue. It is worth pointing out, however, that all students who have commented on the matter have observed that symmetrodonts (e.g., *Kuehneotherium*, *Tinodon*, *Spalacotherium*, *Zhangheotherium*) lack an angular process or, for that matter, any ventral or posteroventral expansion of the dentary in the angular region (e.g., Simpson 1928a, 1929; Prothero 1981; Hu *et al.* 1997); an angular process is also lacking in triconodontids and gobiconodontids. This is distinctly different from the condition (where known) among eupantotheres and peramurans (e.g., *Amphitherium*, *Peramus*, Dryolestidae: see Prothero 1981) and among tribosphenic mammals. We tentatively recognize the development of a posteriorly placed angular process as a derived feature characterizing eupantotheres and tribosphenidans (Trechnotheria of Prothero 1981). This feature is absent in *Spalacolestes*, as it is in *Spalacotherium* and all other symmetrodonts.

A pterygoid crest or pterygoid shelf (Miao 1988; Rowe 1988; Gambarayan & Kielan-Jaworowska 1995) on the medial surface of the mandible may be related to increased importance of the pterygoid muscle in mandibular adduction, translation, and rotation (e.g., Oron & Crompton 1985). The pterygoid crest is lacking in primitive taxa such as *Morganucodon* (in which the medial pterygoid muscle is interpreted to have been small, Crompton & Hylander 1986) and *Kuehneotherium*. Prothero (1981) cited the presence of a pterygoid crest as a synapomorphy of Symmetrodonta (including Spalacotheriidae and Amphidontidae), but this crest enjoys a considerably broader distribution, being present in eupantotheres (e.g., *Laolestes* Simpson, 1927; *Amblotherium* Owen, 1871; see Simpson 1929: 63, 68), triconodontids (Simpson 1928b), gobiconodontids (Jenkins & Schaff 1988), multituberculates (Miao 1988; Gambarayan & Kielan-Jaworowska 1995), and tribosphenidans (Kielan-Jaworowska & Dashzeveg 1989, fig. 20; Sánchez-Villagra & Smith 1997), as well as symmetrodonts (except *Kuehneotherium*). Rowe (1988, 1993)'s Theriiomorpha includes a pterygoid shelf as a diagnostic character (see discussion in Miao 1993). Although the pterygoid crest (and its continuation onto the angle, where present, of the therian dentary) may be developed as a medial shelf (e.g., multituberculates, Marsh 1880; Gambarayan & Kielan-Jaworowska 1995) or inturned process (e.g., some Cretaceous Eutheria, Kielan-Jaworowska *et al.* 1979), the condition among marsupials (commonly termed an inflected angle) has been suggested to be a derived character unique to the group (Sánchez-Villagra & Smith 1997). However, using the definition these authors provide ["a medially inflected angular process may be defined as one that projects inward (lingually) at about 90 degrees with respect to the dorsoventral plane of the mandibular ramus," Sánchez-Villagra & Smith 1997: 120], we observe an inflected angle to be present in *Prokennalestes* (e.g., GI PST 10-5C, 10-6).

In *Spalacotherium*, the pterygoid crest originates just below the mandibular foramen. The crest is incompletely preserved in available specimens, so that its full extent cannot be determined. However, it was greatly expanded and, perhaps, developed a medial process in the region of the mandibular foramen, an unusual feature among early mammals. This clearly was the case with

Spalacolestes. Here the pterygoid crest begins just below the alveolar margin at the junction of horizontal and ascending rami, descending posteroventrally to the region of the mandibular foramen, where it is developed as a large, curving process that encloses a small pocket. The strong development of the pterygoid crest into a process near the mandibular foramen is unusual among early mammals; it is lacking in other symmetrodonts such as *Tinodon* and *Zhangheotherium*. The condition in *Spalacolestes*, in which there clearly is a large, reflected process and the pterygoid crest continues anterodorsally, is undoubtedly unusual and apomorphic. An edentulous dentary that we refer to *Spalacotheroides bridwelli* (FMNH PM 1025) preserves some limited information on the medial side of the jaw in this species. The pterygoid crest clearly originated just below the alveolar margin and extended posteroventrally, as in *Spalacolestes*. The specimen is considerably abraded in the vicinity of the mandibular foramen, and it is unclear whether the pterygoid crest was developed into a process, as in the taxon from Utah. To our knowledge, the only other Mesozoic mammal with a pterygoid crest that extends anterodorsally and nearly reaches the alveolar margin of the dentary is *Prokennalestes* (see Kielan-Jaworowska & Dashzeveg 1989, fig. 20).

A related and noteworthy feature on the medial side of the dentary in *Spalacolestes* is the great size of the pterygoid fossa (we are indebted to Z. Luo for suggesting this to us). In most Mesozoic mammals, such as triconodontids (see Simpson 1928a) and gobiconodontids (see Jenkins & Schaff 1988), the pterygoid fossa extends anteriorly to about the level of the mandibular foramen; in *Spalacolestes*, the pterygoid fossa extends well anterior to the mandibular foramen. Among spalacotheriids, the presumed primitive condition (pterygoid fossa terminates anteriorly adjacent to the mandibular foramen) is present in *Spalacotherium* (see Simpson 1928a) and *Zhangheotherium* (see Hu *et al.* 1997), whereas the pterygoid fossa extends farther anteriorly in *Spalacotheroides* (FMNH PM 1025). The posterior part of the dentary is not known in other taxa; nonetheless, this distribution suggests the possibility that the derived condition may represent a shared, derived feature of North American Spalacotheriidae.

The ventral margin of the dentary in the angular region of *Spalacotherium* is reflected laterally into a "wide, efflected, flange-like masseteric crest," as Simpson (1928a: 102) noted. The same is true, to a greater degree, in *Spalacolestes*. Although the posteroventral margin of the dentary has some lateral reflection in certain triconodonts (Hopson 1994) and gobiconodontids (Jenkins & Schaff 1988), it is not significantly developed in other symmetrodonts or other Mesozoic mammals, and the degree of reflection seen in *Spalacotherium* and (especially) *Spalacolestes* is unusual. The masseter muscle inserts along the ventral and lateral side of the dentary in this region, and the unusual condition in spalacotheriids is likely related to the development or configuration of this muscle (the masseteric fossa is also rather deep in *Spalacotherium* and *Spalacolestes*). Lacking the skull, functional interpretation is limited. However, the mandibular symphysis was probably unfused, as suggested by BM 47748, referred to *Spalacotherium*. The mandible of *Zhangheotherium* was also unfused (see Hu *et al.* 1997), as is the case with most early mammals (Crompton & Hylander 1986). It is likely that mastication in spalacotheriids involved significant components of mandibular rotation and lateral translation: the masseter serves to invert the dorsal border of the hemimandible on which it inserts, and the pterygoid serves to evert it (Oron & Crompton 1985; Crompton 1995). Hence, there is reason to believe that the unusual condition of the pterygoid crest and the lateral reflection of the posteroventral margin of the dentary in spalacotheriids are functionally related features, and that they may indicate some unusual aspect (perhaps strong development) of lateral translation or rotational movement in the masticatory cycle of these mammals, as suggested by consideration of their shearing surfaces (see also Patterson 1956: 57; Crompton 1971; Sigogneau-Russell & Ensom 1998). As has been described for lower molars of North American Spalacotheriidae (Fox 1976; Cifelli & Madsen 1986), upper molars of *Spalacotheridium* and *Spalacolestes* bear obliquely oriented wear striations on both prevallum and postvallum surfaces

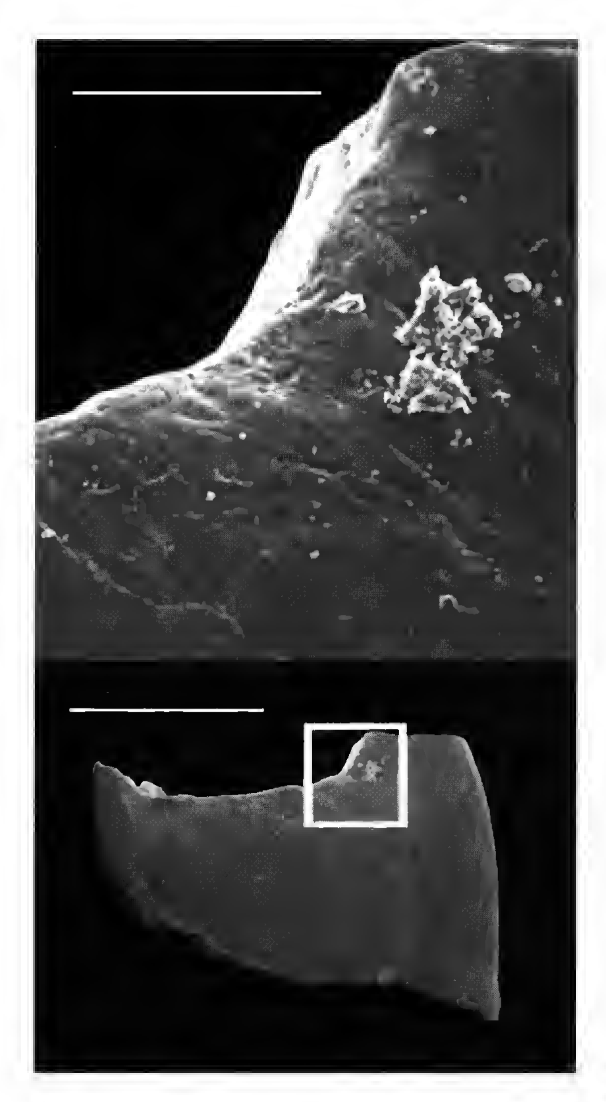


FIG. 18. — Microwear structures in *Spalacolestes cretulablatta* n. gen., n. sp.; bottom, mesial view showing prevallum shearing surface on left M4 (OMNH 30611); box indicates location of enlarged photo, above. Scale bars: top, 0.1 mm; bottom, 1 mm.

(Fig. 18). The relative contributions of lateral translation and rotation of the mandible in the masticatory cycle cannot be determined, although it is likely that both played significant roles.

LOWER MOLARS

We believe it highly probable that the lower tooth series of *Spalacolestes* (and, tentatively, *Spalacotheridium*) included seven molars, as in *Spalacotherium* (see Simpson 1928a; Clemens 1963); four are present in *Tinodon* (see Simpson 1929), six in *Zhangheotherium* (the described specimen is a juvenile and it is possible that not all molars were erupted, see Hu *et al.* 1997), and three to six in *Kuehneotherium*. Based on study of edentulous jaws, the lower part of this range was thought to be most probable for *Kuehneotherium* (see Kermack *et al.* 1968). Study of isolated teeth suggests that as many as six molars may have been present in some individuals (Mills 1984); the most complete alveolar row known for the genus shows that at least five were present on this specimen (Gill 1974). As noted by Patterson (1956), the molar count in symmetrodonts is correlated with angulation between principal cusps: "acute-angled" symmetrodonts are characterized by a high number of molars. On this basis, remaining taxa from the North American Cretaceous (*Spalacotheroides*, *Symmetrodontoides*) probably also had a high number of lower molars, seven being the likely number. Judged by comparison to *Kuehneotherium* and other outgroup taxa, the acute angulation and high molar count of spalacotheriids represents the derived condition.

Individual molar characteristics also set North American Cretaceous taxa and *Spalacotherium* apart from *Kuehneotherium*, *Tinodon*, and certain other symmetrodonts. In *Kuehneotherium* (and probably *Woutersia* as well), as in morganucodontids, precise occlusion is dependent on development of extensive wear facets on corresponding upper and lower molars. In spalacotheriids, however, matching molar surfaces fit more precisely (Crompton & Hylander 1986; Crompton 1995), as they do in tribosphenic therians. In *Tinodon*, as in *Kuehneotherium*, separate wear facets develop on occluding surfaces of the principal cusps, whereas in spalacotheriids, strong crests are developed between the protoconid and lingual cusps, and these form continuous prevallid and postvallid shearing surfaces (Crompton & Jenkins 1967; Crompton 1971). The condition in *Zhangheotherium* is uncertain, but it has been described as differing from other spalacotheriids in having rounded, conical cusps that lack connecting crests (Hu *et al.* 1997), strongly suggesting that it is similar to *Tinodon* or *Kuehneotherium* in lacking continuous shearing surfaces.

The cingulum and cingular cusps also are variable among symmetrodonts. In *Kuehneotherium* and *Tinodon*, only a lingual cingulum is present on the lower molars, the distolingual (talonid) cusp is moderately well developed, and two mesial cingular cusps are present (Crompton & Jenkins 1967). A cingulum is lacking from lower molars of *Zhangheotherium* (see Hu *et al.* 1997); it is incomplete labially, at least, in most other primitive mammals, such as *Woutersia* (see Sigogneau-Russell & Hahn 1995), *Morganucodon* (see Kermack *et al.* 1973), and Amphidontidae (see Simpson 1929; Trofimov 1980). In spalacotheriids, a single mesial cusp is present and the talonid is somewhat smaller than it is in *Tinodon* and *Kuehneotherium* (Crompton & Jenkins 1967). In addition, all spalacotheriids – with the exception of *Zhangheotherium* and the apparent exception of *Spalacotheroides* (see above) – have a complete labial cingulum on the lower molars. In all of these features, Spalacotheriidae appear to be derived with respect to remaining symmetrodonts (see Sigogneau-Russell & Ensom 1998 for discussion of the distribution and variability in the development of the lower molar cingulum among symmetrodonts).

Spalacotheriidae also appear to be unusual among Mesozoic mammals in the manner in which their lower molars interlock (we are grateful to Z. Luo for pointing this out to us). In morganucodontids and docodonts, the distalmost molar cusp, cusp d, fits between cusps b and e of the succeeding tooth (see, e.g., Crompton & Jenkins 1968); presumably modified arrangements are present in other taxa, such as *Kuehneotherium*, gobiconodontids, and triconodontids (see Luo 1994; Kielan-Jaworowska & Dashzeveg 1998). In spalacotheriids, the distal cingular cusp (which appears to be homologous with cusp d) is placed lingual to the mesial cingular cusp (which occupies a similar position to cusp e and may be homologous with it) of the following tooth, and the mesial cingular cusp fits into an embayment of the cingulum that is labial to cusp d of the preceding tooth.

Within Spalacotheriidae, taxa from the North American Cretaceous appear to be advanced with respect to *Spalacotherium* in having more acutely angled, higher crowned lower molar trigonids; *Spalacotheridium* is the least extreme in this regard (the condition is unclear in *Spalacotheroides*, but it is probably safe to say that its lower molars are more acutely angled than are those of *Spalacotherium*). In species of *Spalacolestes* and *Symmetrodontoides*, the paraconid and paracristid are distinctly lower than the metaconid and metacristid on all lower molars (except m7, which in *Spalacolestes* at least, lacks a metaconid); in species of *Symmetrodontoides*, the height differential is accentuated. The cusps are subequally developed in *Spalacotheridium*, *Spalacotherium* (see Simpson 1928a), and *Tinodon*, except on m1, where the paraconid is slightly smaller (e.g., USNM 2131). In *Woutersia* (see Sigogneau-Russell & Hahn 1995), by contrast, the paraconid is the taller of the two; in *Kuehneotherium* (see Kermack *et al.* 1968; Mills 1984), the condition is variable and the cusps should be considered subequal in development. We concur with Sigogneau-Russell & Ensom (1998) in believing that paraconid and metaconid were primitively subequal in Spalacotheriidae (as they are, for example, in *Zhangheotherium*), and conclude that the condition in *Spalacolestes* and *Symmetrodontoides* is derived. Both of the last-mentioned genera are characterized by the presence of posterior lower molars that are labiolingually expanded, owing to a relatively elongate paracristid and lingually placed paraconid.

Upper molars

As with the lower molars, the upper molars of Spalacotheriidae are more acute-angled than those of primitive taxa such as *Kuehneotherium* (see Kermack *et al.* 1968) and *Tinodon* (see Simpson 1929). Upper molars of *Spalacolestes*, *Symmetrodontoides*, and *Spalacotheridium*, at least, are more acute-angled (assumed to represent the derived condition) than those of *Spalacotherium* or *Zhangheotherium*. The single upper molar of *Spalacotheroides* illustrated by Patterson (1956, fig. 1) probably represents one of the mesial loci; other specimens (e.g., FMNH PM 1133, 1236) are distinctly more acute. *Microderson* (see Sigogneau-Russell 1991b), which resembles North American taxa in several other respects, is also rather acutely angled. The

paracone on upper molars of *Spalacotherium* and *Zhangheotherium*, like that of North American Spalacotheriidae, is extremely tall relative to the condition seen in most outgroup taxa (e.g., *Tinodon, Kuehneotherium*). We suspect that paracone height will prove to be a useful character for or within Spalacotheriidae when its distribution becomes better known.

Recent studies (e.g., Hu *et al.* 1997; Sigogneau-Russell & Ensom 1998) have followed Patterson (1956) in identifying the mesiolabial cusp on upper molars of *Spalacotherium* (lacking at mesial loci, see Butler 1939) as the stylocone, or cusp B; hence, the more lingually placed cusp on the preparacrista is a neomorph by comparison to outgroup taxa such as *Kuehneotherium*. This cusp (termed B_1 by Hu *et al.* 1997) is also present in *Zhangheotherium* and *Spalacotheroides* (except the mesial molar, FMNH PM 1235, figured by Patterson 1956): is it primitive for Spalacotheriidae, or a derived feature characterizing these three genera? Other features, such as the presence of fewer than six upper molars and the ?lack of continuous shearing surfaces, suggest that *Zhangheotherium* represents the sister-taxon to remaining Spalacotheriidae, in turn providing some tentative evidence that the presence of this cusp may be primitive for the family. Under this interpretation, the absence of cusp B_1 in North American Spalacotheriidae (except *Spalacotheroides*) would represent a loss. Patterson (1956) also suggested that the mesialmost stylar cusp of *Spalacotheroides*, which lies mesial to the preparacrista, is a new cusp not present in *Spalacotherium*, and that it represents one of several, independent acquisitions of a parastylar cusp in therian mammals. Interpretation of this feature is problematic. A parastylar cusp is lacking in *Zhangheotherium* (see Hu *et al.* 1997). The single known upper molar of *Tinodon* (YPM 13637) lacks the parastylar region of the tooth, although Crompton (1971) restored *Tinodon* with a parastylar cusp. A cusp in this position is present in *Kuehneotherium* (see Kermack *et al.* 1968). Regardless, the prominent, hooklike parastylar region seen on anterior molars of *Symmetrodontoides* (see Fox 1985), *Spalacotheridium*, and *Spalacolestes* would appear to be an advanced condition by comparison to remaining taxa (see Sigogneau-Russell & Ensom 1998). Of the remaining upper molar cusps, cusp C is well marked in outgroup taxa such as *Kuehneotherium* and *Tinodon*, and is present in *Zhangheotherium*, *Spalacotherium*, *Microderson*, and *Spalacotheroides*. This suggests that the absence of cusp C in taxa from the medial and Late Cretaceous of North America represents an advanced condition. As described by Patterson (1956), *Spalacotheroides* has two distolabially placed stylar cusps (a metastyle and one that is more mesially placed at the margin of the stylar shelf), whereas only one is present in *Spalacotherium* (see Clemens 1963: 376). A single distolabial cusp (metastyle) is seen in *Kuehneotherium* (see Kermack *et al.* 1968), *Microderson* (see Sigogneau-Russell 1991b), and *Zhangheotherium* (cusp "D" of Hu *et al.* 1997). Positional evidence favors homology of the distalmost cusp (metastyle; see above) on upper molars of these taxa, suggesting that the more mesial cusp of *Spalacotheroides* is a neomorph. Taxa from the medial and Late Cretaceous of North America have the distolabially placed metastylar cusp and, more mesially, a mesiodistally expanded cusp at the margin of the stylar shelf. We tentatively regard the latter as homologous with the mesial of the two distal stylar cusps in *Spalacotheroides* (which we interpret to be stylar cusp "D" of Sigogneau-Russell & Ensom 1998), and its presence as an advanced feature characterizing North American Spalacotheriidae. The condition in *Spalacolestes*, *Spalacotheridium*, and *Symmetrodontoides*, in which the mesial of the two cusps is strongly developed on mesial molars, represents a more derived condition. A strongly developed distal stylar cusp is also present in the enigmatic *Thereuodon* from the Early Cretaceous of Morocco and England, which is otherwise so different as to be non-comparable (see Sigogneau-Russell 1989; Sigogneau-Russell & Ensom 1998).

In *Spalacotheroides*, as in remaining North American Spalacotheriidae, the preparacrista is markedly lower than the postparacrista, particularly on mesial molars. Judged by comparison with *Tinodon* and *Kuehneotherium*, this appears to be a derived condition, but the distribution of the character is difficult to determine from avail-

able literature. The preparacrista is clearly lower than the postparacrista in *Microderson*, whereas the crests appear to be subequal in development in *Spalacotherium* (see Simpson 1928a, fig. 34) and *Zhangheotherium* (see Hu *et al.* 1997, fig. 2). As noted by Fox (1985), the stylocone is so small in *Symmetrodontoides* that it is indistinguishable in teeth that have been subject to even moderate wear. The stylocone is also small in *Spalacolestes* and *Spalacotheridium*. Comparison with remaining Spalacotheriidae (*Spalacotherium*, *Spalacotheroides*, *Zhangheotherium*), as well as *Kuehneotherium*, *Woutersia*, and *Tinodon* (in which the stylocone is prominent), indicates that the stylocone has probably undergone reduction in the taxa from the medial and Late Cretaceous of North America (see also Sigogneau-Russell & Ensom 1998).

Comparison of upper molar shape and proportions in Spalacotheriidae is problematic because series are known for so few taxa and because, as shown above, coronal profile and degree of symmetry varies according to tooth position. M1/1 of *Spalacotherium* is considerably smaller than succeeding molars, whereas in *Spalacotheridium* and *Spalacolestes*, M1/1 is relatively much larger (e.g., Figs 6, 11, compare with Butler 1939, fig. 7). Insufficient basis for comparison leaves us uncertain as to the significance and polarity of this feature. *Spalacotheridium*, *Symmetrodontoides*, and *Spalacolestes* have an M4 that is remarkably symmetrical. Past this tooth position, molar size decreases, and the last molar is significantly smaller than its predecessor. Comparison to *Spalacotherium* suggests that these may be advanced conditions. In *Spalacotherium*, posterior molars sequentially develop a parastylar lobe that, on the last tooth, projects strongly. A small parastylar lobe is present on posterior molars of *Spalacotheridium* but lacking in *Spalacolestes* and *Symmetrodontoides*, suggesting reduction in the latter two taxa. All three North American genera differ from *Spalacotherium* in having the paracone progressively placed more distally on posterior molars (vaguely recalling a similar shift in the protocone of posterior upper molars in tribosphenic mammals). In terms of crown relief, *Spalacolestes* and *Symmetrodontoides* differ from *Spalacotheridium* in having a relatively deeper trigon basin. *Microderson* also appears to have a deep trigon basin, but this appearance is due to the fact that the paracone is extremely tall in this taxon. In remaining Spalacotheriidae, the trigon is much shallower than in *Spalacolestes* and *Symmetrodontoides*, so we interpret a shallow trigon basis as most probably representing the primitive condition.

Relationships and concluding remarks

To summarize, the limited data in hand suggest that recently described *Zhangheotherium* is primitive in several respects, and represents the sister-taxon to remaining Spalacotheriidae (Fig. 19). *Spalacotherium*, in turn, evidently is the sister-taxon to North American Spalacotheriidae. (We have omitted *Microderson*, known by a single upper molar, from our phylogeny. As noted above, this Moroccan taxon resembles one or another of the North American spalacotheriids in several respects, but the significance of these resemblances cannot be evaluated with data in hand; see discussion in Sigogneau-Russell 1991b.) Of the North American spalacotheriids, the geologically oldest, *Spalacotheroides bridwelli* from the Aptian-Albian, appears to retain the most number of primitive features, such as the presence of cusps B_1 and C on the upper molars (assuming that the presence of these cusps is primitive for Spalacotheriidae). *S. bridwelli* is unusual within the family in that the labial cingulum of lower molars is apparently incomplete (see Fox 1976). If this condition is correctly interpreted and not simply a matter of preservation (the holotype, FMNH PM 933, includes the only known lower molar of this species, and it may be abraded), then we believe *S. bridwelli* to be autapomorphic in this respect. Of remaining genera, neither *Spalacotheridium* nor *Spalacolestes* (two species each) is characterized by known synapomorphies, unless the slight elongation of the paracristid on lower molars of *Spalacolestes cretulablatta* and *S. inconcinnus* represents a shared derived character. *Symmetrodontoides* (three species) is the geologically youngest and most advanced member of the family, characterized by labiolingually expanded posterior lower molars.

Some members of the Mussentuchit local fauna,

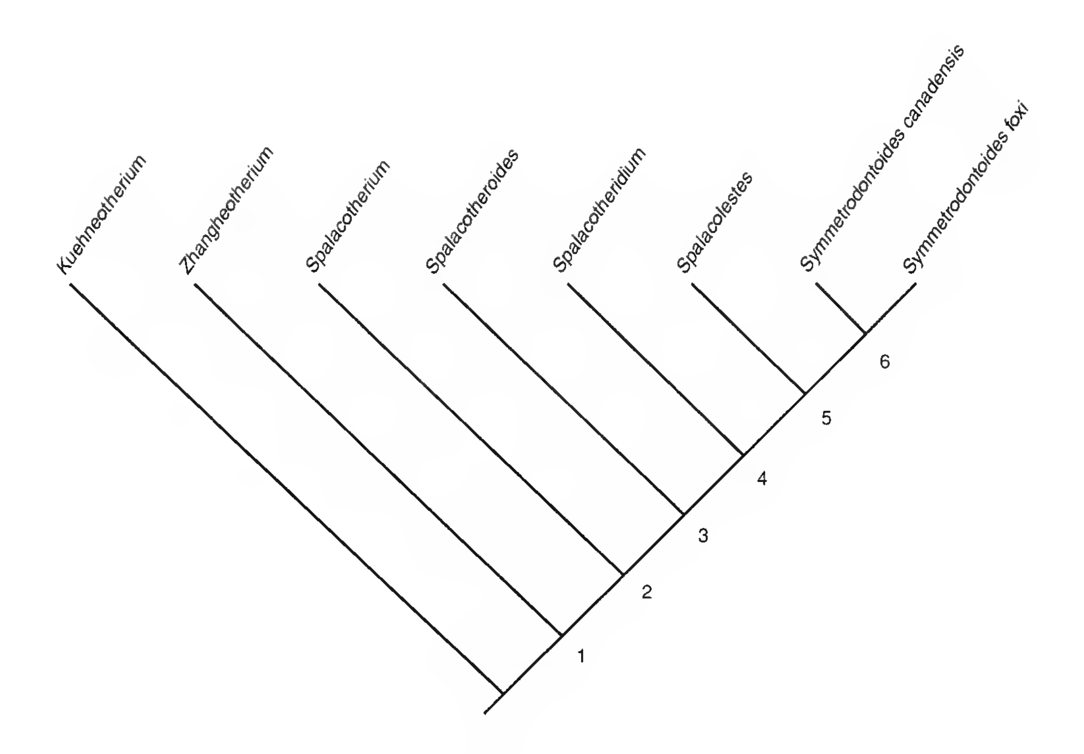


FIG. 19. — Hypothesis of relationships among Spalacotheriidae; *Kuehneotherium* included as outgroup, *Microderson* omitted because of insufficient data; additional North American species (*Symmetrodontoides oligodontos, Spalacotheridium mckennai, Spalacolestes inconcinnus*) not included because they are poorly known and, based on present knowledge, add no detail to the phylogeny presented. Characters at nodes (see discussion in text): **1**, (Spalacotheriidae) molars acutely angled; ?gain extra cusp (B1 of Hu *et al.* 1997) on upper molars; single mesial cingular cusp on lower molars; reduce distal cingular cusp (talonid) on lower molars; unique lower molar interlocking mechanism, whereby the distal cingular cusp of one molar is placed labial to the mesial cingular cusp of the succeeding tooth; **2**, six or more upper and lower molars present; ?pterygoid crest strongly developed in region of mandibular foramen (known only for *Spalacotherium* and *Spalacolestes*); continuous prevallum and postvallum shearing surfaces on molars; ?posteroinferior border of dentary inflected (known only for *Spalacotherium* and *Spalacolestes*), ?labial cingulum complete on lower molars (lacking in *Spalacotheroides*); **3**, (Spalacolestinae) meckelian groove lost; pterygoid crest extends anterodorsally to near occlusal margin of dentary, with pterygoid fossa extending well anterior to mandibular foramen (known only for *Spalacotheroides, Spalacolestes*); molars higher crowned, more acutely angled; upper molars with parastyle (see Patterson 1956), distal stylar cusp, and preparacrista lower than postparacrista (anterior loci); **4**, upper molars with reduced stylocone, distal stylar cusp enlarged, strong, hooklike parastyle (anterior loci), M4 strongly symmetrical, C cusp lost; M6 reduced, with paracone posteriorly placed (condition uncertain in *Spalacotheroides, Symmetrodontoides*), **5**, ?coronoid facet lost (condition unknown in *Spalacotheroides, Spalacotheridium, Symmetrodontoides*); upper molars with deep trigon basin, reduced parastyle (distal loci; condition unknown in *Spalacotheroides*); lower molars with paraconid and paracristid lower than metaconid and protocristid, respectively; paraconid of distal lower molars lingually placed, with paracristid distinctly longer than protocristid; upper molars with cingulum complete lingually; **6**, height differential between paraconid and metaconid on posterior lower molars pronounced; posterior lower molars broadened; m1 with taller paraconid and paracristid; M1-2 more acutely-angled, with less bulbous paracone base and more tightly arced or folded lingual face to paracone.

notably several groups of dinosaurs, appear to represent elements of a mid-Cretaceous immigration event from Asia (Cifelli *et al.* 1997). Origin of other taxa is more problematic. North American Cretaceous triconodontids, for example, appear to represent a monophyletic group, but their origin within the known Jurassic diversity of the family (both New and Old World) is uncertain (see Cifelli *et al.* 1998). If North American Spalacotheriidae are monophyletic, as we suggest, then their biogeographic ties antedate the hypothesized mid-Cretaceous interchange, as they would represent a group that was established on the continent by the Aptian-Albian, at least. Preliminary studies of somewhat older (Barremian) dinosaurs from Utah

(Kirkland *et al.* 1997) and elsewhere in North America (Norman 1998) suggest a link with the penecontemporaneous or slightly older Wealden assemblage of western Europe. *Spalacotherium*, the suggested sister-taxon to North American spalacotheriids, occurs in the Late Jurassic or earliest Cretaceous (Purbeck, see Clemens *et al.* 1979; Allen & Wimbledon 1991) to Early Cretaceous (Wealden) of England (Clemens & Lees 1971) and Spain (Krebs 1985), providing corroborative support for the suggestion of faunal continuity between North America and Europe prior to the Aptian-Albian (see, e.g., Norman 1998).

The Mussentuchit local fauna includes the most diverse assemblage of symmetrodonts known from North America, with at least four species present. There is no clear temporal trend in North American spalacotheriid diversity: one species is known from the Aptian-Albian (Patterson 1955, 1956), one from the Cenomanian (J. G. Eaton, pers. comm.), two from the Turonian (Cifelli 1990), and one each from two local faunas of the early Campanian (Fox 1976; Cifelli & Madsen 1986). In view of the tiny size of most known species, part of this may well be due to collecting biases, but it is notable that spalacotheriids are not only diverse but extremely abundant in the Mussentuchit local fauna, where they vastly outnumber all other mammals except multituberculates: evidently they were a rather successful group in the mid-Cretaceous of central Utah. Interestingly, the distribution of species is decidedly non-random in the upper part of the Cedar Mountain Formation. Of the thirty-two sites sampled extensively for microvertebrates, only eight (Fig. 1) yielded remains of Spalacotheriidae. The overwhelming majority of specimens referable to *Spalacolestes cretulablatta* was recovered from a single, heavily-sampled site, with fewer numbers from three other sites. *Spalacotheridium noblei*, though less abundant, is far more extensive in distribution: it is known from seven sites, and is quite rare at the major locality that produced such a wealth of specimens referable to *S. cretulablatta*. *S. inconcinnus*, on the other hand, is a rare species known from a single, poorly sampled locality – it is not present at the most heavily sampled site or, for that matter, anywhere else. Given the fact that all sites are located in a narrow stratigraphic interval and are believed to be essentially isochronous (Cifelli *et al.* 1997, 1999), we consider it unlikely that these differences are temporal in nature. All of the sites occur in fluvial overbank deposits. Although the depositional setting appears to be rather similar between sites, we attribute the distribution of Spalacotheriidae in the upper part of the Cedar Mountain Formation as being due to differences in habitat preference among species, with *Spalacolestes cretulablatta* and, particularly, *S. inconcinnus*, being characterized by a far greater degree of habitat specificity than was evidently the case for *Spalacotheridium noblei*.

Acknowledgements

We acknowledge with heartfelt thanks the numerous individuals who generously supplied us with unpublished information, access to specimens, advice, comments on an earlier version of this manuscript, or other help: W. A. Clemens, Jr., Bob Emry, Susan Evans, Richard C. Fox, Jacques Gauthier, Jerry Hooker, Jim Hopson, Zofia Kielan-Jaworowska, Jay Lillegraven, Zhexi Luo, Bill Turnbull, and, most especially, Denise Sigogneau-Russell, who provided much help in all of the categories listed. It is a pleasure to thank the Judd family of Castle Dale, Utah, for their continuing and unfailing help to field parties through the years; to Beth Larson, Randy Nydam, Nick Czaplewski, and Kent Smith for their help in field work; and to Tom Rasmussen and the Bureau of Land Management for their continuing cooperation. Scanning electron micrographs were done by Cindy Gordon at the Samuel Roberts Noble Electron Microscopy Laboratory, University of Oklahoma, and Randy Nydam helped with digital image processing. Figures 2, 3, 6, and 11 were drafted by Nick Czaplewski; Figures 8, 9 were prepared by Glenn Traughber; and Figure 1 was drafted by Coral McCallister. Comparative study and critical intereaction with colleagues was greatly facilitated by a Professeur Associé appointment for R. L. Cifelli at the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, and the support of Drs Philippe Taquet, Philippe

Janvier, and Christian de Muizon is acknowledged with heartfelt thanks. This research was conducted under the following grants to RLC: National Geographic Society 5021-92 and National Science Foundation BSR 8906992, DEB 9401094, and DEB-9870173.

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Submitted for publication on 20 July 1998;
accepted on 19 November 1998.

Composition en acides aminés d'os de mammifères fossiles de deux sites du Plio-Pléistocène d'Angola. Comparaison avec la conservation de la phase minérale

Hélène DAVID
Laboratoire de Paléontologie, Université Paris-XI, Bât. 504, F-91405 Orsay cedex (France)
Laboratoire d'Anthropologie, Université Bordeaux-I,
avenue des Facultés, F-33405 Talence cedex (France)

Yannicke Dauphin & Pascale GAUTRET
Laboratoire de Paléontologie, EP 1748 du CNRS, Université Paris-XI,
Bât. 504, F-91405 Orsay cedex (France)

Martin PICKFORD
Laboratoire de Paléontologie, UMR 8569 du CNRS, Muséum national d'Histoire naturelle,
8 rue de Buffon, F-75231 Paris cedex 05 (France)
Chaire de Paléoanthropologie et de Préhistoire, Collège de France,
11 place Marcelin-Berthelot, F-75005 Paris (France)

Brigitte SENUT
Laboratoire de Paléontologie, UMR 8569 du CNRS, Muséum national d'Histoire naturelle,
8 rue de Buffon, F-75231 Paris cedex 05 (France)

David H., Dauphin Y., Gautret P., Pickford M. & Senut B. 1999. — Composition en acides aminés d'os de mammifères fossiles de deux sites du Plio-Pléistocène d'Angola. Comparaison avec la conservation de la phase minérale. *Geodiversitas* (21) 2 : 215-227.

MOTS CLÉS
Plio-Pléistocène,
Angola,
Theropithecus,
Bos,
os,
FTIR,
acides aminés.

RÉSUMÉ
La comparaison des paramètres microstructuraux et de composition (phases organique et minérale) d'os de mammifères actuels et fossiles (Plio-Pléistocène d'Angola) montre le caractère différentiel de la diagenèse. Malgré une conservation microstructurale globalement bonne, les compositions chimiques des phases minérales sont modifiées (enrichissement en Ca, appauvrissement en Mg). Très peu de matrice organique est conservée. Les phases organiques solubles et insolubles sont également diversement altérées, la composition en acides aminés de la phase soluble semblant mieux conservée que celle de la phase insoluble.

ASBTRACT
Composition in amino-acids of fossil mammalian bones from two Plio-Pleistocene Angolan sites. Comparison with the preservation of the mineral phase.
Comparison of the microstructural parameters and composition (organic and mineral phases) of modern and fossil mammal bones (Plio-Pleistocene of Angola) show the differential character of diagenesis. Despite excellent preservation of the microstructure, the chemical composition of the mineral phases has been modified (enriched in Ca, reduction of Mg). The amount of preserved organic matrix is greatly reduced. The amino-acid composition of the soluble organic phase appears to be better preserved than that of the insoluble phase.

KEY WORDS
Plio-Pleistocene,
Angola,
Theropithecus,
Bos,
bone,
FTIR,
amino-acids.

INTRODUCTION

L'abondance des phases organiques dans l'os actuel semble un facteur favorable à leur conservation chez les fossiles, et les données relatives à leur composition devraient être très abondantes. Cependant, de telles informations demeurent ponctuelles car, malgré cette circonstance apparemment favorable à des analyses extensives, les techniques analytiques de la phase organique nécessitent la déminéralisation de l'os. Or, ceci implique la destruction du seul paramètre généralement étudié par le paléontologiste, et considéré encore actuellement comme le plus, sinon le seul, réellement important et informatif : la morphologie. Second point qui limite considérablement la portée des données sur les os fossiles : les études sont très spécialisées, soit par la technique utilisée (diffraction X, immunologie...), soit par le composant choisi (phase minérale, composition de l'ostéocalcine...). Bien que l'os soit un matériau complexe, rares sont les travaux prenant simultanément en compte les paramètres de la phase minérale et de la phase organique. Enfin, à cause de la spécialisation de plus en plus poussée des laboratoires et de la complexité croissante des techniques analytiques, la comparaison de la diagenèse des phases organiques et de celle de la phase minérale demeure un problème rarement abordé. Les données sur les phases organiques fossiles sont donc encore réduites, malgré leur potentiel informatif très vaste (apport à la reconstitution de la phylogénie, du paléoenvironnement, histoire de la fossilisation, compréhension des processus de formation des sites...). La diversité des âges et de la géologie des sites fossilifères est telle que des « lois » régissant la fossilisation et tous les phénomènes connexes ne pourront être établies qu'à partir de très nombreuses données.
Une étude préalable ayant mis en évidence la présence de sucres dans un astragale de bovidé récolté dans un site angolais plio-pléistocène (David *et al.* 1996), l'analyse de ce spécimen a été poursuivie afin d'obtenir des données sur la diagenèse comparée des phases minérales et organiques. Un site fossilifère voisin, de même âge mais de sédimentologie différente, a fourni des os de primates, susceptibles de fournir des informations supplémentaires sur la fossilisation et la diagenèse.

TRAVAUX ANTÉRIEURS

Les travaux sur la structure, la minéralogie et la composition de l'os actuel sont trop nombreux pour être cités. Très rapidement, les auteurs ont abandonné les analyses globales au profit d'une caractérisation des composants protéiques isolés, pour en déterminer la composition ou le séquençage. Parmi les paramètres caractéristiques des phases organiques, les acides aminés semblent avoir été parmi les premiers étudiés, notamment à cause des particularités de composition du collagène. Or, ce dernier constitue environ 90 % de la phase protéique de l'os. Toutefois, dès 1965, Glimcher & Katz mettaient en évidence les pro-

blèmes posés par la solubilisation plus ou moins grande du collagène dans divers solvants et acides.
Chez les fossiles, les premières analyses détaillées semblent dues à Abelson (1956) sur du matériel dévonien. La comparaison de la composition en acides aminés de spécimens appartenant à des taxons variés, et venant de sites d'âges différents, montre une grande variabilité (Armstrong & Halstead Tarlo 1966 ; Dungworth *et al.* 1974 ; Wyckoff & Davidson 1976 ; Davidson *et al.* 1978 ; Von Endt & Ortner 1982 ; Cohen-Solal *et al.* 1987). En réalité, cette variabilité doit être supérieure à ce qui ressort de l'examen de la littérature, car seuls les résultats « positifs », c'est-à-dire les analyses dans lesquelles les acides aminés ont pu être identifiés, sont généralement publiés. Or, certains sites fossiles fournissent des os contenant encore de la phase organique, mais les spectres d'acides aminés ne sont pas toujours interprétables (Montgelard *et al.* 1997 ; Dauphin 1998). De plus, dans la plupart des cas, seule la phase organique insoluble (assimilée au collagène malgré les variations pouvant être dues au produit utilisé pour la déminéralisation de l'os), est prise en compte. Outre le collagène, l'albumine et l'ostéocalcine sont les protéines le plus souvent identifiées chez les fossiles ou subfossiles (Tuross *et al.* 1980 ; Lowenstein 1981 ; Huq *et al.* 1985 ; Montgelard 1992). Il s'agit en fait des protéines les mieux caractérisées dans l'os actuel car il y aurait au moins deux cents protéines non collagéniques (ou NCP) (Delmas *et al.* 1984). L'acide γ-carboxyglutamique, longtemps considéré comme caractéristique de l'ostéocalcine, a été recherché chez les fossiles. Toutefois, les interprétations qui découlent de sa présence ou de son absence quant à la « bonne conservation » de l'os doivent être pondérées. D'une part, l'ostéocalcine est parfois en quantité négligeable, comme dans l'os humain. D'autre part, dans l'os adulte, toutes les protéines non collagéniques sont déjà fortement dégradées (Termine 1988), ce qui restreint fortement la probabilité de sa conservation chez les fossiles. Enfin, l'acide γ-carboxyglutamique a été extrait et identifié dans les squelettes de coraux, et est probablement également présent dans les tests de mollusques (Hamilton & Zerner 1983).

MATÉRIEL ET MÉTHODES

Matériel

Les spécimens actuels de références sont constitués par un tibia de bœuf (congelé et sec), un humérus de *Papio anubis* (Cercopithecoidea d'Ouganda, ayant séjourné en forêt pendant une durée indéterminée) et du collagène commercial de type I (Sigma).
Les deux sites fossilifères, situés sur le plateau d'Humpata (sud de l'Angola) sont datés du Plio-Pléistocène. Le fragment d'astragale de bovidé provient des découvertes effectuées lors d'une campagne de l'Angola Palaeontology Expedition (Pickford *et al.* 1992, 1994). Il a été récolté dans des remplissages de fissures de la carrière de Cangalongue III, composées de brèches grossières, contenant de nombreux fragments de stalagmites recimentés par des travertins. Les fragments de côtes et de vertèbres de *Theropithecus* (primates Cercopithocoidea) viennent du gisement de Tchiua, dont les remplissages sont formés de brèches à grains très fins. Cette formation a été interprétée comme du guano calcifié de chauve-souris.
Il convient de signaler que la diversité des os ne peut guère provoquer de biais majeurs dans la comparaison, compte tenu du niveau d'observation utilisé dans ces analyses.

Méthodes

Microstructures
Des cassures brutes et traitées ont été observées au microscope électronique à balayage. Les os actuels ont été soumis à des protéolyses enzymatiques, afin d'éliminer partiellement l'abondante matrice organique qui tend à masquer les structures. De la trypsine et de l'alcalase ont été utilisées car elles sont peu spécifiques. Les surfaces polies des os fossiles ont été légèrement décalcifiées à l'acide formique.

Composition globale
La composition minéralogique et la présence de phases organiques ont été déterminées par spectrométrie infrarouge à transformée de Fourier (FTIR). Après décontamination des polluants organiques à l'hypochlorite de sodium, les os sont rincés à l'eau Milli-Q et séchés à température

ordinaire. Ils sont ensuite finement broyés. Les poudres d'os mélangées à du KBr ont été analysées sur un spectromètre FTIR Perkin Elmer 1600, équipé d'un accessoire à réflexion diffuse (DRIFT). Le nombre de balayages est de soixante-quatre (soit un temps d'analyse supérieur à quatre minutes par spectre), dans une gamme de longueurs d'onde allant de 450 à 4000 cm^{-1} (Dauphin 1993). Le système est maintenu sous atmosphère d'azote afin de réduire les bandes dues aux CO_2 et H_2O atmosphériques.

Analyse chimique élémentaire
La composition chimique a été déterminée par microanalyse localisée (spectrométrie dispersive en énergie ou EDS). Le système utilisé, Link An 10000 couplé à un microscope électronique Philips (SEM 505) (Université Paris-XI-Orsay), possède un programme spécialement conçu pour l'analyse des surfaces rugueuses. Par une préparation adaptée des spécimens, il est aisé d'identifier les divers composants d'un fossile (tissu, sédiment). La préparation des échantillons, les conditions d'analyse et le traitement statistique sont similaires à ceux précédemment décrits (Dauphin 1997). Dans les spécimens actuels, les teneurs de certains éléments chimiques sont inférieures à la limite de détection de la microsonde (Fe ou Mn par exemple). Toutefois, les valeurs obtenues sont indiquées, car ces éléments sont de bons indicateurs de la diagenèse, leurs teneurs dans les fossiles étant souvent supérieures à la limite de détection de la microsonde.

Composition en acides aminés
Les os ont été décontaminés à l'hypochlorite de sodium, puis nettoyés pendant quelques minutes aux ultrasons afin de décoller les particules et débris divers qui pouvaient subsister, notamment sur les fossiles. Après rinçage à l'eau Milli-Q, ils ont été séchés à température ambiante.
Les poudres résultant du broyage ont été décalcifiées à l'acide acétique sous un pH constant de 4. Les phases solubles (MOS) et insolubles (MOI) ont été séparées par centrifugation. La phase soluble a été dessalée par ultrafiltration avec de l'eau Milli-Q sur une membrane dont le seuil de coupure est de 3 kDa. La phase insoluble a été dessalée par centrifugations successives dans de l'eau Milli-Q. Les phases soluble et insoluble ont été lyophilisées.
Après hydrolyse dans une solution HCl 6N pendant vingt-quatre heures à 110 °C sous atmosphère d'azote, la dérivation PITC a été effectuée car elle permet la détection des amines secondaires. La composition en acides aminés a été obtenue par chromatographie HPLC en phase inverse, sur une colonne Nucleosyl C18, avec un éluent d'acide orthophosphorique et NaOH à pH 6,4 et un gradient d'acétonitrile. Le détecteur est réglé à 254 nm. Rappelons que l'hydrolyse utilisée détruit les acides aminés soufrés (cystéine et méthionine), ainsi que le tryptophane. L'acide γ-carboxyglutamique, qui nécessite une hydrolyse particulière de type alcalin, n'a pas été recherché, les matrices organiques extraites des os fossiles étant en très faibles quantités.

Points isoélectriques
À partir des compositions en acides aminés, on peut calculer le point isoélectrique moyen (pI) d'une phase organique (Sillero & Ribeiro 1989), ce qui permet d'estimer son degré d'acidité. Dans la formule utilisée par ces auteurs, les acides aspartique, glutamique, la cystéine libre, la tyrosine, l'histidine, la lysine et l'arginine sont pris en compte. Cette méthode indirecte présente l'avantage de pouvoir être appliquée sur les matrices soluble et insoluble, ce qui n'est pas le cas des méthodes directes chromatographique (*chromatofocussing*) ou électrophorétique (*isoelectric focussing*), plus précises car elles fournissent l'ensemble des points isoélectriques des divers composés. De plus, le calcul à partir des pourcentages d'acides aminés permet de connaître le pI des phases solubles même lorsque les quantités recueillies sont minimes.

RÉSULTATS

CONTRÔLE DE L'ÉTAT DE CONSERVATION GÉNÉRALE DES OS

L'observation de la microstructure est une première étape dans le contrôle de l'état de conservation d'un fossile. Elle est récemment devenue cruciale, car certains champignons contiennent

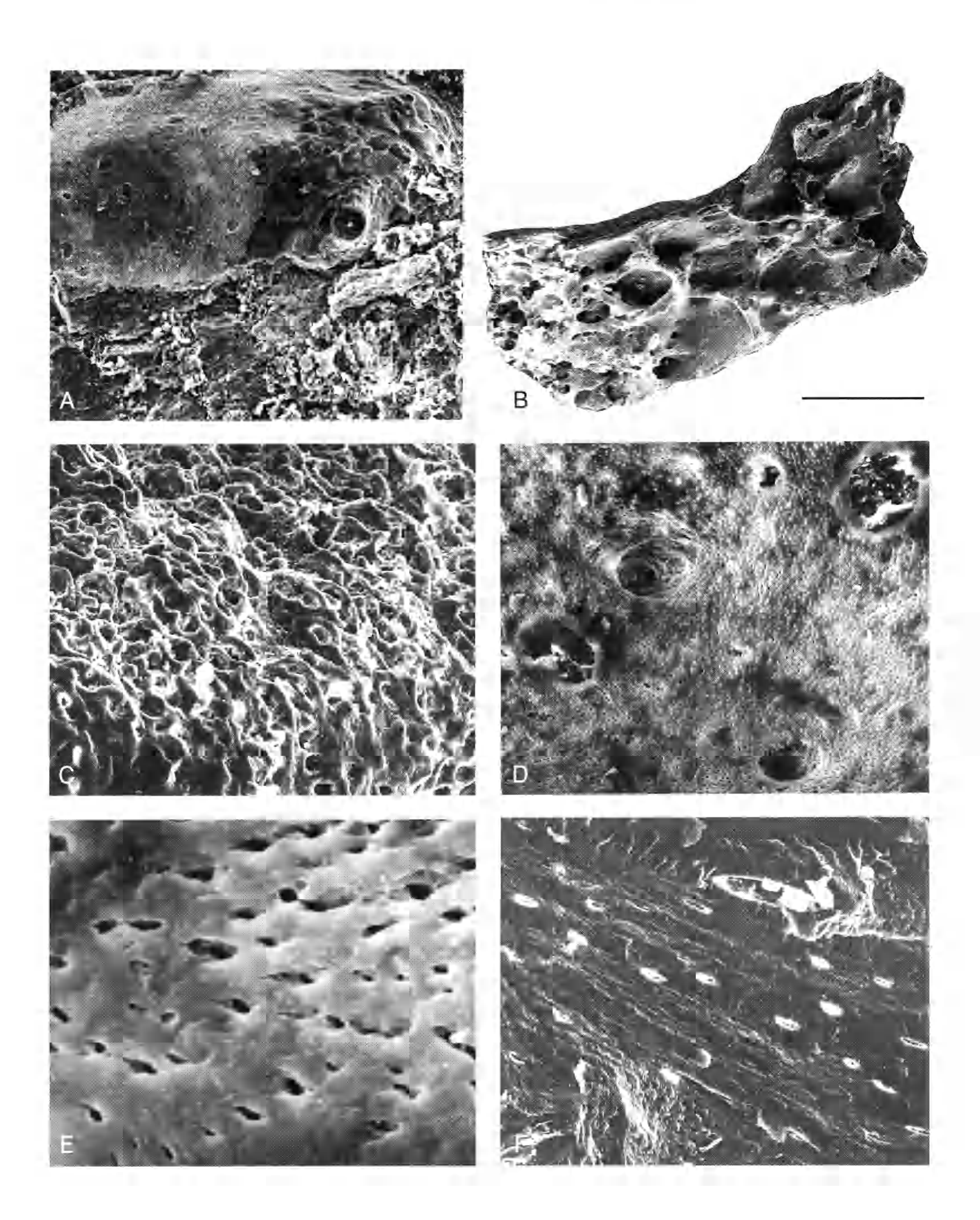


FIG. 1 — **A**, surface externe altérée dans une cassure ancienne de l'astragale du bovidé fossile de Cangalongue. Échantillon non traité ; **B**, vue d'un fragment de vertèbre de *Theropithecus*, Cercopithécoidea (Tchiua), après un nettoyage insuffisant pour détruire un éventuel sédiment présent dans les cavités (acide formique 5 %, 15 s) ; **C**, surface altérée d'un fragment de côte de *Theropithecus*, Cercopithécoidea montrant l'os spongieux après disparition du périoste ; cassure traitée à l'acide formique 5 %, 15 s ; **D**, coupe oblique montrant la paroi des trabécules dans l'os spongieux d'un fragment de côte de *Theropithecus* ; même spécimen que Fig. 3 ; **E**, détail de la précédente ; **F**, lamelles osseuses dans une coupe oblique d'un fragment de côte de *Theropithecus* ; cassure traitée à l'acide formique 5 %, 15 s. Échelle : A, 160 µm ; B, 3 mm ; C, 90 µm ; D, F, 100 µm ; E, 10 µm.

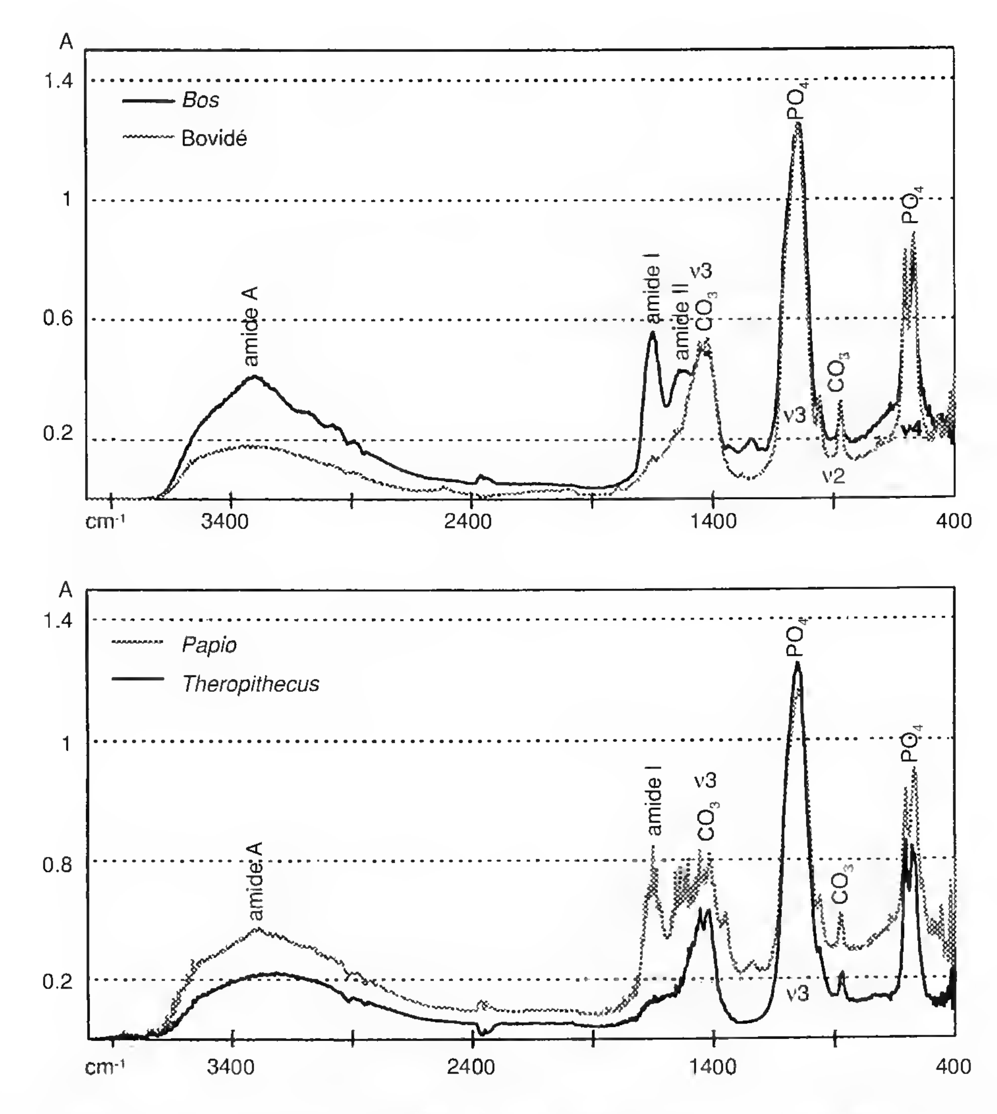


FIG. 2. — Spectres infrarouges des os actuels (*Bos* et *Papio*, Cercopithecoidea) et fossiles (bovidé et *Theropithecus*) montrant que les os fossiles sont conservés en apatite, et la diminution de leur quantité de matière organique.

des acides aminés jusqu'ici considérés comme caractéristiques du collagène (hydroxyproline et hydroxylysine) (Celerin *et al.* 1995).
Les sections diversement orientées réalisées dans l'os de bœuf actuel observé au microscope électronique à balayage après une protéolyse enzymatique montrent la structure lamellaire, le système haversien et les zones en « contreplaqué » (David *et al.* 1996). Macroscopiquement altéré (Fig. 1A), le fragment d'astragale de bovidé de Cangalongue ne comporte pas de remplissage secondaire dans les cavités naturelles de l'os, ni de trace indiquant l'activité de micro-organismes (David *et al.* 1996). Les risques de contamination en matrice organique d'origine exogène apparaissent ainsi réduits. Les cavités des vertèbres de *Theropithecus* ne sont pas comblées (Fig. 1B). Sur les fragments de côtes, les altérations de l'os périostique (Fig. 1C) permettent d'observer l'os spongieux sous-jacent, ainsi que des structures lamellaires dans les zones plus internes. Des lacunes ostéocytiques sont parfois présentes. La disposition des fibres de collagène minéralisées est conservée sur les parois des trabécules

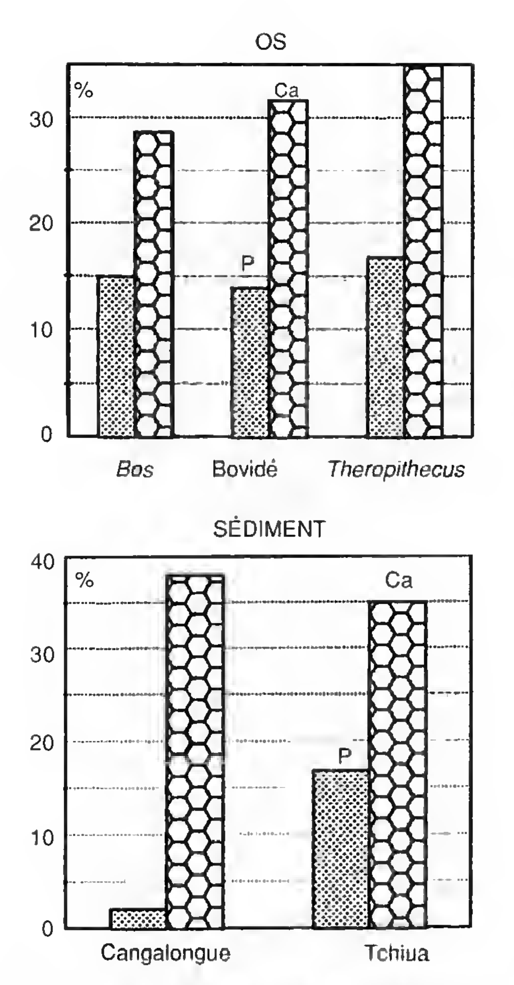
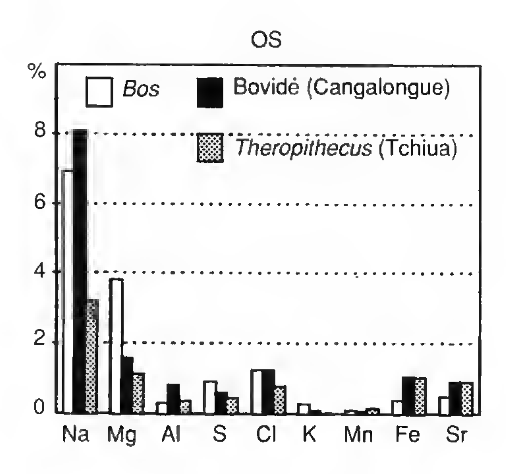


FIG. 3. — Teneurs en éléments majeurs : P et Ca, des os actuels et fossiles, et du sédiment encaissant.



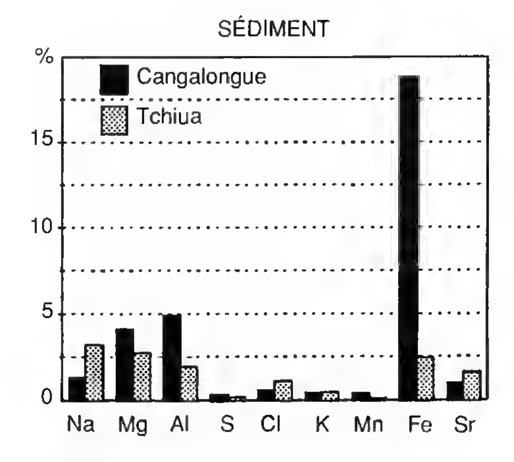


FIG. 4. — Teneurs en éléments mineurs des os actuels et fossiles, et du sédiment encaissant.

(Fig. 1D, E). La structure en lamelles est également visible (Fig. 1F).

COMPOSITION GLOBALE ET ÉLÉMENTAIRE

Les spectres infrarouges montrent que dans les deux sites, les os sont en apatite, avec des modifications modérées (Fig. 2). Termine & Posner (1966) ont mis au point un mode de calcul de la cristallinité (*spliting fraction*) de l'os à partir des intensités relatives des bandes du doublet ν4 PO_4. Le taux moyen de cristallinité de l'os atteint 0,10 pour le bœuf actuel et 0,11 pour *Papio* ; celui du bovidé fossile est supérieur à 0,14 tandis que chez *Theropithecus* il est égal à 0,08. Les variations du taux de cristallinité des os actuels dépendent de l'âge de l'animal : faible chez l'animal jeune, il sera plus élevé chez un animal âgé. Chez les fossiles, ces variations originelles sont généralement masquées par les modifications diagénétiques. Que la cristallinité augmente ou diminue, la cause de ces variations reste la plupart du temps indéterminée : disparition de l'os amorphe, augmentation de la phase cristalline aux dépens de la phase amorphe, ou augmentation de la cristallinité de la phase initialement déjà cristalline. Stutman *et al.* (1965) ont montré que la position et l'intensité des bandes ν1, ν3 et ν4 dépendaient du type d'apatite : hydroxyapatite, chloroapatite et fluoroapatite. Si F est normalement en quantité insuffisante dans l'os actuel pour altérer les fré-

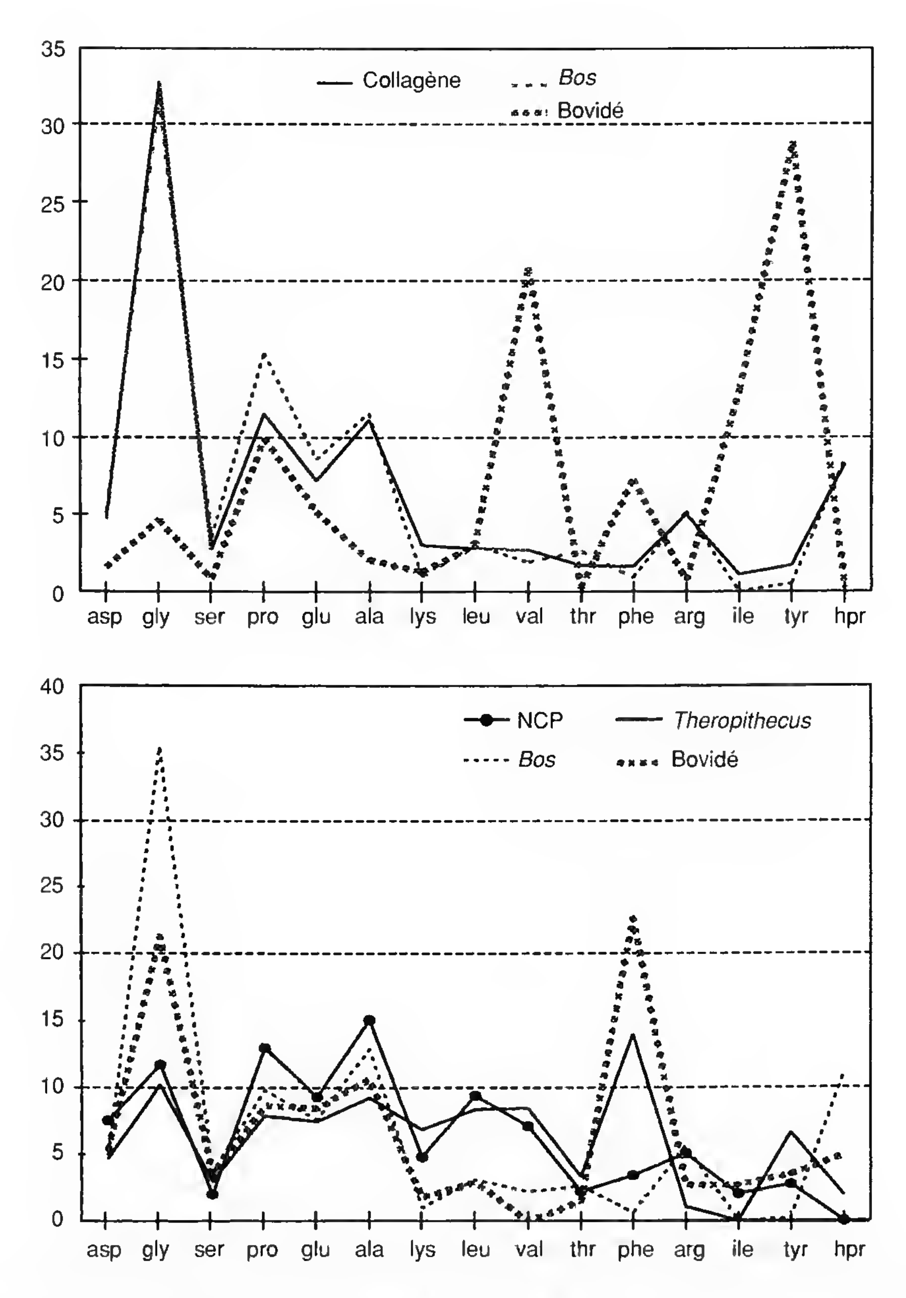


FIG. 5. — Composition en acides aminés (%) des phases insolubles (en haut) et solubles (en bas) des os actuels et fossiles de Cangalongue et de Tchiua. Les compositions du collagène et des protéines non collagéniques (NCP d'après von Endt & Ortner 1982) sont figurées.

quences de ces bandes, il est généralement admis qu'il est en quantité importante dans tous les os fossiles. Toutefois, d'après ces critères, les os fossiles ne sont pas enrichis en F.
Les différences de composition des sédiments (l'un calcaire, l'autre phosphaté), n'apparaissent pas dans les spectres, ce qui confirme l'absence d'un remplissage important des cavités osseuses. La phase organique, encore présente chez les fossiles (amides A, I et II), y est modifiée en quan-

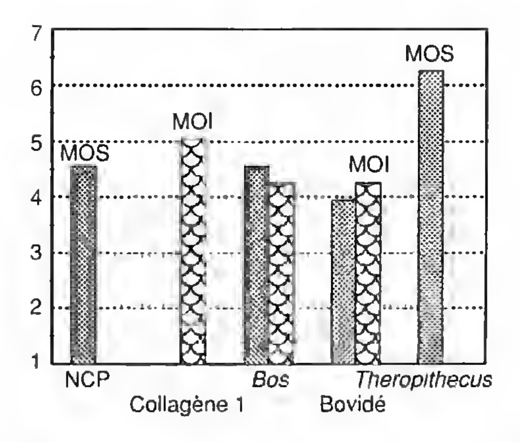


Fig. 6. — Points isoélectriques moyens calculés d'après les compositions en acides aminés par la méthode de Sillero & Ribeiro 1989.

tité (bandes moins intenses) et en qualité (absence de certaines bandes).
Les os fossiles sont tous deux enrichis en Ca (Fig. 3), *Theropithecus* étant en outre plus riche en P que le bovidé. Le rapport en poids Ca/P de l'os de bœuf actuel est voisin de 1,96, celui de *Papio* atteint 2,02. Chez les fossiles, ces rapports sont supérieurs : 2,08 pour *Theropithecus* et 2,30 pour le bovidé. Les teneurs en éléments mineurs ne montrent pas de modifications importantes. Malgré la grande différence de quantité en Fe des deux sédiments (Fig. 4), cette disparité n'est pas transcrite dans les fossiles puisque les teneurs des os sont similaires dans les deux sites (Fig. 4). Le sédiment de Cangalongue est calcaire, et plus riche en Mg et Al que Tchiua (Figs 3, 4).

Composition en acides aminés

Phase organique insoluble (Fig. 5)

La composition de la matrice insoluble extraite de l'os de bœuf est identique à celle du collagène commercial de référence (type I). La matrice insoluble du bovidé fossile est très différente de celle de l'os actuel, mais la plupart des pics a été identifiée. Les teneurs en glycine, hydroxyproline, proline et alanine sont plus faibles que dans l'actuel, les teneurs en tyrosine, valine et isoleucine sont plus élevées. Deux pics non identifiés sont présents. La composition de la matrice insoluble de *Theropithecus* est beaucoup moins claire : de nombreux pics ne sont pas identifiables avec certitude et le spectre n'est pas représenté dans la Figure 5. Dans la zone correspondant à la succession thréonine, alanine, histidine et proline, on trouve seulement un large dôme. Les deux pics non identifiés chez le bovidé existent également.

Phase organique soluble (Fig. 5)

À titre de comparaison, la composition des protéines non collagéniques (NCP) est figurée (Von Endt & Ortner 1982). Peu abondantes (10 % de la matrice organique de l'os : Hauschka & Wians 1989), ces protéines non collagéniques sont cependant très variées. Nombre d'entre elles ne sont pas encore identifiées, et certaines sont connues seulement partiellement. La composition de la phase soluble extraite de l'os de bœuf actuel est relativement similaire à celle de la phase insoluble ; cette similitude est partiellement due à la mise en solution partielle du collagène (Weiner & Bar-Yosef 1990). Par rapport à la composition des protéines non collagéniques (NCP), la matrice soluble du bœuf est trop riche en hydroxyproline et en glycine, trop pauvre en leucine et valine.
La matrice soluble du bovidé fossile se caractérise par une très forte teneur en phenylalanine et une baisse sensible des quantités de glycine et d'hydroxyproline. Pratiquement tous les pics sont identifiables. La matrice de *Theropithecus* est également riche en phénylalanine, glycine, alanine et proline, sans atteindre toutefois des valeurs comparables à celle du bovidé. Les teneurs en hydroxyproline sont nulles. En outre, le spectre est très clair et tous les pics sont identifiables.

Points isoélectriques (pI) moyens des matrices

Les matrices organiques de l'os, collagènes et NCP sont acides (Fig. 5). Il en est de même pour les matrices extraites de l'os de bœuf actuel. Si le pI moyen de la phase soluble de l'os de bœuf est similaire à celui des NCP, le pI de la phase insoluble du bœuf est légèrement plus acide que celui du collagène de type I. La phase soluble du bovidé fossile est devenue un peu plus acide que l'insoluble. Quant à la phase soluble du *Theropithecus*, elle atteint un pI supérieur à 6 (Fig. 6).

DISCUSSION

Ces deux exemples sont bien évidemment insuffisants pour en tirer des conclusions définitives sur les processus de fossilisation des os. D'une part seuls deux sites sont pris en considération, d'autre part les paramètres analysés sont trop peu nombreux. Cependant, pour chaque composant, ils sont suffisants pour révéler certains points communs et certaines différences, avec les études publiées.

Composition globale

La composition globale des os fossiles des deux sites de Cangalongue et de Tchiua montre que les os y sont conservés en apatite. Toutefois, la diagenèse n'est pas absente puisque des paramètres tels que les teneurs en Ca, en P, la cristallinité et les teneurs globales en matrices organiques sont altérés. La composition des phases organiques est également altérée. Très peu de matrice organique a pu être extraite des os fossiles des deux sites. Ainsi que le fait remarquer Glimcher (1993) : « … *the original volume occupied by the organic matrix must have been replaced by new inorganic material (crystals and possibly amorphous solid phases) formed during the period of fossilization and after the death of the animal* […] *it seems unreasonable to assume that the atom and ion consituents in the mineral phase of the skeleton and tooth tissues of the fossil specimen are those which were present at the time of the animal's death.* » L'utilisation abusive des paramètres géochimiques pour la reconstitution des paléoenvironnements doit une fois encore être signalée, que ces paramètres dérivent de la phase minérale ou de la phase organique. L'une des tendances actuelles en ce domaine consiste à « remplacer » les données issues de l'analyse de la phase minérale par celle de la phase organique, qui serait moins sensible à la diagenèse. Or, dans la plupart des cas, cette matrice organique est très altérée en qualité et en quantité. Et lorsque sa quantité semble voisine de celle des os actuels, elle est au moins partiellement exogène (Montgelard *et al.* 1996 ; Dauphin 1998). Dans le cas des fossiles d'Angola, seules les analyses de la composition en acides aminés et les données qui en découlent (pI moyens) ont été étudiées. Les interprétations sont donc limitées, car de nombreux paramètres restent inconnus : masses moléculaires, composition en acides aminés et pI de chaque composant par exemple. En fait, si *a priori* l'abondance naturelle des phases organiques dans l'os semble être un facteur favorable à leur conservation, elle est surtout un des facteurs principaux de leur destruction. D'une part, les cellules contiennent de nombreuses protéases qui sont libérées à la mort de l'animal, contribuant ainsi à la dégradation rapide et à la destruction de la phase organique. D'autre part, les bactéries, rencontrant un milieu nutritif riche, sont très actives.

Conservation différentielle des phases organiques

Dans les spécimens angolais, d'après leurs compositions en acides aminés, les phases organiques insolubles sont plus altérées que les phases solubles. Paradoxalement, les compositions en acides aminés des phases solubles du bovidé fossile et du *Theropithecus* sont plus proches de celle du collagène que les phases insolubles des mêmes spécimens. La comparaison avec les données de la littérature n'est pas immédiate, notamment à cause de la diversité des techniques d'analyses disponibles pour les acides aminés. Il est en effet pratiquement impossible d'obtenir, avec une seule hydrolyse et une seule dérivation, un spectre contenant tous les acides aminés. Toutefois, une telle similitude a déjà été signalée dans des os subfossiles (Hedges *et al.* 1980). Dans cette étude cependant, les amines secondaires (dont l'hydroxyproline, l'un des éléments les plus caractéristiques du collagène) ne sont pas mentionnées. Il est probable qu'au cours de la diagenèse, les fibres de collagène se fragmentent. Ce phénomène peut être comparé aux procédures expérimentales permettant de couper les longues fibres en peptides, couramment pratiquées sur le collagène de type I. Ces techniques ont pour but de rendre possible l'utilisation des méthodes classiques d'analyse des phases solubles (chromatographie liquide et électrophorèse notamment) sur une phase initiale insoluble (Rossi *et al.* 1996).

On peut noter la similitude entre les bovidés actuel et fossile, qui tous deux, présentent une phase soluble très riche en acides aminés caractéristiques du collagène. Le collagène solubilisé par les processus de décalcification apparaît donc moins sensible aux altérations diagénétiques que le collagène non solubilisé. Ces différences de comportement pourraient être dues à son degré d'association avec la phase minérale. On peut rapprocher ces observations de celle de Masters (1987), qui avait déjà reconnu la conservation différentielle des composants de l'os, les NCP étant les mieux conservées.

RÔLE DU SÉDIMENT

De nombreux facteurs interviennent pendant la fossilisation des restes squelettiques ; en outre, les processus diagénétiques sont permanents entre le stade de l'enfouissement et la découverte du fossile. Parmi ces facteurs, la taille des os est à considérer. Bien que les études sur le sujet demeurent limitées, la composition chimique élémentaire de la zone externe d'un os de grand mammifère est plus modifiée que ses zones internes (Williams & Marlow 1987 ; Williams & Potts 1988). L'influence de la composition du sédiment est dans ce cas évidente, puisque le périmètre externe des os est enrichi en éléments chimiques très abondants dans le sédiment environnant. Toutefois, l'influence du sédiment est variable selon les sites car bien que le sédiment de Cangalongue soit beaucoup plus riche en Fe que celui de Tchiua, les os ont à peu près les mêmes teneurs en Fe. Une étude détaillée de l'évolution des teneurs en Fe de l'extérieur vers l'intérieur des os n'a pas été faite. L'éventuel remplissage de la cavité médullaire peut augmenter les modifications diagénétiques.

Enfin, en dépit d'un sédiment dont la composition est plus proche de celle de l'os à Tchiua qu'à Cangalongue, les phases organiques du *Theropithecus* sont plus modifiées que celles du bovidé. Il faut noter que les dimensions des fragments de vertèbres et de côtes du *Theropithecus* étaient nettement inférieures à celles du fragment de bovidé. L'absence de données détaillées sur les sédiments et le contexte géologique des deux sites ne permet pas de faire des comparaisons détaillées.

Il convient donc de noter que, en dépit d'une microstructure et d'une minéralogie conservées, la diagenèse est présente dans ces os fossiles. Il semble important d'insister sur le fait que les composés minéraux et organiques d'une part, et les phases organiques solubles et insolubles d'autre part, ont des réactions différentes aux processus diagénétiques. Ainsi, dans le cas des fossiles d'Angola, les données peuvent apparaître contradictoires : la composition en acides aminés indique une diagenèse plutôt modérée dans le cas du bovidé, alors que l'estimation de la quantité de sa phase organique montre une forte diagenèse. Il apparaît donc de plus en plus que l'état de conservation des phases minérales ou organiques ne peut être établi à partir de l'analyse d'un seul type de composé. Et ce d'autant plus que, rappelons le, certains produits considérés comme caractéristiques de l'os (collagène et acide γ-carboxyglutamique par exemple) sont maintenant connus dans des taxons variés.

La connaissance de la suite d'événements qui préside à la formation d'un gisement de fossiles, ainsi que la compréhension des altérations diagénétiques, ne pourra être atteinte que par des séries d'analyses progressives, allant des caractères les plus généraux (composition minéralogique, présence de phases organiques) jusqu'aux plus détaillés (composition en acides aminés ou en monosaccharides de chaque protéine par exemple). Le problème majeur de telles études est que les fractionnements successifs nécessaires à une telle identification impliquent que ces phases organiques soient conservées en quantité suffisante dans les os.

Remerciements

Les auteurs tiennent à remercier les nombreuses personnes, en France (Prof. Y. Coppens et P. Taquet) et en Angola (Dr S. Aço, Mission française de coopération à Luanda ; Instituto Nacional do Patrimonio Cultural ; Museu Regional de Huila, Lubango) qui ont permis la réalisation de la campagne de terrain en Angola en 1990. Les commentaires détaillés du Prof. M. J. Glimcher (The Children's Hospital, Boston) ainsi que ceux de deux autres rapporteurs anonymes ont été très utiles pour l'amélioration de ce manuscrit.

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Soumis pour publication le 10 mars 1998 ;
accepté le 15 septembre 1998.

New stem giraffoid ruminants from the early and middle Miocene of Namibia

Jorge MORALES
Departamento de Paleobiología, Museo Nacional de Ciencias Naturales,
CSIC, José Gutierrez Abascal 2,
E-28006, Madrid (Spain)

Dolores SORIA
Departamento de Paleobiología, Museo Nacional de Ciencias Naturales,
CSIC, José Gutierrez Abascal 2,
E-28006, Madrid (Spain)

Martin PICKFORD
Chaire de Paléoanthropologie et de Préhistoire, Collège de France,
11 place Marcelin-Berthelot, F-75005, Paris (France)
Laboratoire de Paléontologie, UMR 8569 du CNRS, Muséum national d'Histoire naturelle
8 rue de Buffon, F-75231 Paris cedex 05 (France)

Morales J., Soria D. & Pickford M. 1999. — New stem giraffoid ruminants from the early and middle Miocene of Namibia. *Geodiversitas* (21) 2 : 229-253.

ABSTRACT
At the early and middle Miocene localities of the Sperrgebiet, Namibia, new material of climacoceratid ruminants have been collected recently. From Elisabethfeld we describe new material belonging to *Propalaeoryx austroafricanus* Stromer, 1926, together with a new genus and species of climacoceratid *Sperrgebietomeryx wardi* n. gen., n. sp., a species without frontal appendages close to *Propalaeoryx* and to primitive early Miocene European ruminants such as *Andegameryx*. From the locality of Arrisdrift, we define another new genus and species of climacoceratid with frontal appendages, *Orangemeryx hendey* n. gen., n. sp., characterized by its complex tined frontal apophyses. Comparison of the dentition and postcranial skeleton of this genus and those of *Sperrgebietomeryx* suggests a close phylogenetic relationships between them.

KEY WORDS
Ruminantia,
Giraffoidea,
Climacoceratidae,
Miocene,
Namibia.

RÉSUMÉ

Nouveaux ruminants giraffoïdes du Miocène ancien et moyen de Namibie.

Dans les localités du Miocène inférieur et moyen de la Sperrgebiet en Namibie, de nouveaux restes de ruminants Climacoceratidae ont été récemment récoltés. Un nouveau matériel provenant d'Elisabethfeld appartenant à *Propalaeoryx austroafricanus* Stromer, 1926 est décrit, ainsi qu'un nouveau genre et une nouvelle espèce du Climacoceratidae, *Sperrgebietomeryx wardi* n. gen., n. sp., espèce ne possédant pas d'appendices frontaux, proche de *Propalaeoryx* et des ruminants primitifs du Miocène inférieur européen, comme *Andegameryx*. À Arrisdrift, nous décrivons un autre genre et une autre espèce de Climacoceratidae avec des appendices frontaux, *Orangemeryx hendeyi*, qui se caractérise par ses apophyses frontales complexes. Les comparaisons entre la dentition et le squelette postcrânien de ce genre et de ceux de *Sperrgebietomeryx* suggèrent une proche parenté phylogénétique entre les deux.

MOTS CLÉS
Ruminantia,
Giraffoidea,
Climacoceratidae,
Miocène,
Namibie.

INTRODUCTION

This is the second report on the ruminants of the early and middle Miocene of Namibia collected by the Namibia Palaeontology Expedition. The first paper dealt with the small bovid *Namibiomeryx senuti* Morales *et al.*, 1995. In this article we describe the giraffoids from the same region.

Two new genera of giraffoids recovered from the sites of Elisabethfeld and Arrisdrift in southern Namibia (Fig. 1) reveal a great deal about the origins of this superfamily of ruminants. The new climacoceratid giraffoids lack frontal apophyses, and occur in the early Miocene deposits at Elisabethfeld and other sites in the northern part of the Sperrgebiet. *Sperrgebietomeryx* is closely related to primitive late Oligocene European ruminants such as *Andegameryx* Ginsburg *et al.*, 1994, and lies close to the root of the group which subsequently developed apophyses, the Giraffoidea. *Sperrgebietomeryx* occurs in the same strata as another sperrgebietomerycine, the genus *Propalaeoryx* Stromer, 1926.

Basal middle Miocene deposits at Arrisdrift have yielded abundant remains of a new genus of climacoceratid, *Orangemeryx*, a climacoceratine

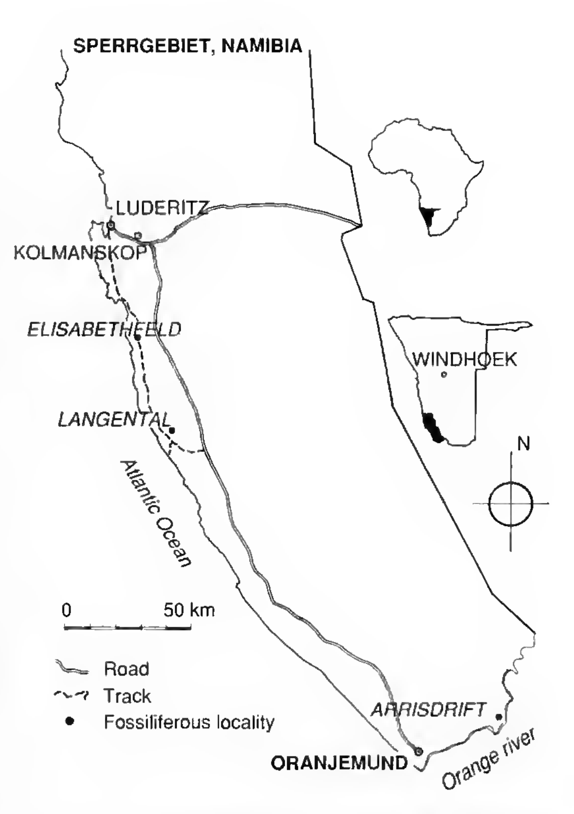


FIG. 1. — Geographical location of Arrisdrift (early middle Miocene) and Langental and Elisabethfeld (early Miocene) in the Sperrgebiet, southern Namibia.

with tined apophyses. Examination of the skull and postcranial skeleton of this genus and those of *Sperrgebietomeryx* suggests that the Arrisdrift species may well be the descendant of the Elisabethfeld one.

The transition from primitive pecorans to climacoceratids with apophyses thus appears to have occurred in Africa subsequent to colonization of this continent by pecorans from Eurasia.

GEOLOGICAL SETTING

Elisabethfeld

The early Miocene site of Elisabethfeld (Stromer 1926) occupies one of a series of pre-Miocene valleys which used to drain into the Atlantic Ocean from the region of the present-day Namib Sand Sea. As a result of a worldwide rise in sea-level during the early Miocene the transient sediments in the valleys stopped moving, and further sedimentation occurred in the drowned valleys. At Elisabethfeld, fine-grained red limey silts accumulated in a plain that lay between the Grillental and one of its southern tributaries which had cut through Proterozoic rocks. These red silts, which are often overprinted with pedogenic features, were incised and then buried by green silts, sands and conglomerates. These fluviatile beds are overlain by a fine-grained palaeodune sequence (Greenman 1966, 1970; Corbett 1989). Unconformably overlying the early Miocene sediments is a two metre thick travertine which has invaded the upper portion of the aeolianite. Fragments of this travertine have been incorporated into a younger set of aeolianites which crop out extensively in the area, often filling palaeo-valleys cut into the early Miocene sediments.

At the base of one of the green, pebbly-sand channel infillings cropping out as a low cliff and immediately overlying the basal red limey silts, the partial skeleton of a ruminant was observed by Drs J. Ward and I. Corbett in June, 1993. The specimen was photographed and left *in situ* for later excavation. In August, 1993, Drs M. Pickford and B. Senut visited the site with J. Ward and excavated the skeleton. It was evident that at least 1 cm of sediment had been removed, principally by sand-blasting, since the photographs had been taken two months previously. A mandible with the cheekteeth in place in June had eroded so that only the ventral margin of the jaw was left in August.

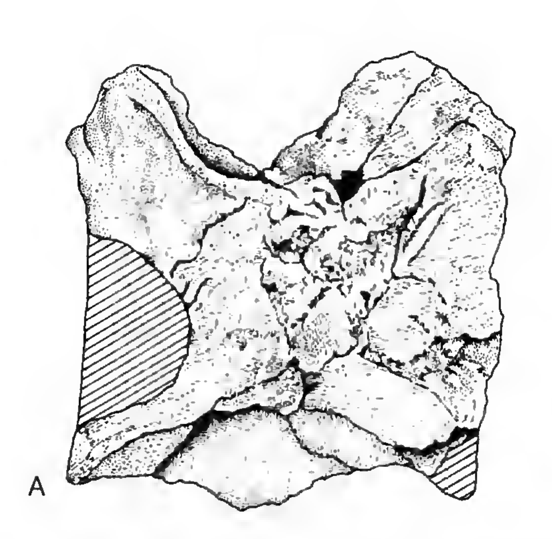
The associated fauna indicates that the Elisabethfeld skeleton is of early Miocene age. The site correlates broadly with the localities of Songhor and Koru, Kenya, and is thus interpreted to be about 20-21 Ma old (Faunal Set I of Pickford 1981).

Arrisdrift

The site of Arrisdrift occurs in a lateral channel of the Proto-Orange located about 1 km east of the present-day channel of the river. Fossiliferous sediments lie at an altitude of about 41 m above mean sea-level, infilling a low channel carved into the Gariep Group of Late Proterozoic age. The channel is filled with a complex cut-and-fill sequence of sediments ranging in grain size from conglomerates to clays, the latter representing clay-drapes deposited during periods when the Arrisdrift channel was cut off from the main river. During periods of high water, the channel would be active, so that numerous scour and fill episodes occurred, and can be seen in superposition in the excavation.

During periods of low water level, the channel was effectively isolated from the main stream and would have been a quiet pool of water. This channel lay close to sea-level, as indicated by the presence of serpulid worm tubes in abundance, even to the extent of forming serpulid reefs. Today these invertebrates live in brackish water in estuarine settings. There can be little doubt that at the beginning of the Middle Miocene, some 17.5-17 Ma ago, sea-level was some 41 m above present day levels.

The site of Arrisdrift, like the earlier ones in the northern Sperrgebiet, owes its formation to the world-wide rise in sea-level that occurred at the end of the early Miocene, which caused the back-ponding of sediments within the Proto-Orange valley. The difference in ages of the fossil sites in the northern and southern Sperrgebiet indicate that the rise in sea-level was relatively slow, the highest stand being reached some 2-3 Ma later than the onset of rising sea-levels.



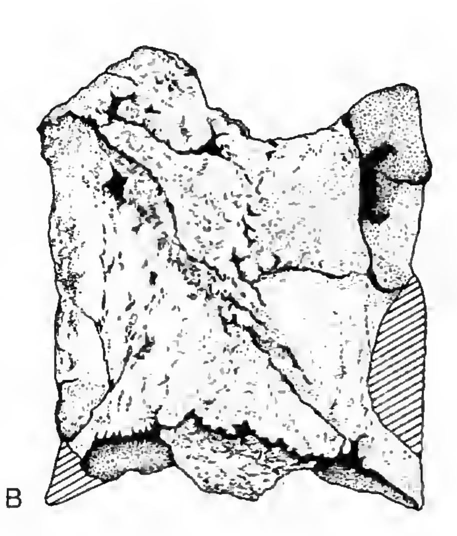


FIG. 2. — Atlas of *Sperrgebietomeryx wardi* n. gen., n. sp. (EF 37'92); **A**, dorsal view; **B**, ventral view. Scale bar: 20 mm.

This scenario is confirmed by the discovery of early Miocene mammals at Auchas, another Proto-Orange deposit, in sediments 32-37 m above present-day mean sea-level, or some 10 m lower than the deposits at Arrisdrift.

By the time that sea-levels dropped again later in the middle Miocene, the Proto-Orange river had abandoned some of its meander loops and was following a less sinuous course towards the coast. When incision occurred following lowering of base-levels, the early and middle Miocene sediments deposited in many of the abandoned loops were left high and dry.

The fauna associated with *Orangemeryx* is early middle Miocene in age, correlating closely with European zone MN4 (De Bruijn *et al.* 1992) and with the sites of Buluk and Maboko in Kenya, assigned to Faunal Set PIII (Pickford 1981). It is probably about 17.5-17 Ma (Pickford 1994).

SYSTEMATIC PALEONTOLOGY

Suborder RUMINANTIA Scopoli, 1777
Superfamily GIRAFFOIDEA Simpson, 1931

Family CLIMACOCERATIDAE Hamilton, 1978
(= CLIMACOCERIDAE Hamilton, 1978)

DIAGNOSIS. — Ruminants of medium to large size characterised by the tendency – in relation to other ruminants of the same age – for elongation of the neck (including the atlas) and limbs. Distal epiphysis of the metatarsal with open gully. Dentition with a clear hypsodont tendency. Palaeomeryx fold in lower molars moderate or suppressed, hypoconid isolated and lobe of m3 simple.

SPERRGEBIETOMERYCINAE n. subfam.

TYPE GENUS. — *Sperrgebietomeryx* n. gen.

DIAGNOSIS. — Climacoceratidae without cranial protuberances. Cranium with wide frontals, sagittal crest and nuchals strongly defined. Dentition moderately hypsodont. Premolar series elongate. Lower molars with strong stylids and moderate paleomeryx fold. Upper molars with very strong styles and late union of the internal lobes with the outer wall.

Sperrgebietomeryx n. gen.

TYPE SPECIES. — *Sperrgebietomeryx wardi* n. sp.

DIAGNOSIS. — The same as for the type species.

Sperrgebietomeryx wardi n. sp.

cf. *Strogulognathus sansaniensis* Filhol (Stromer 1926).

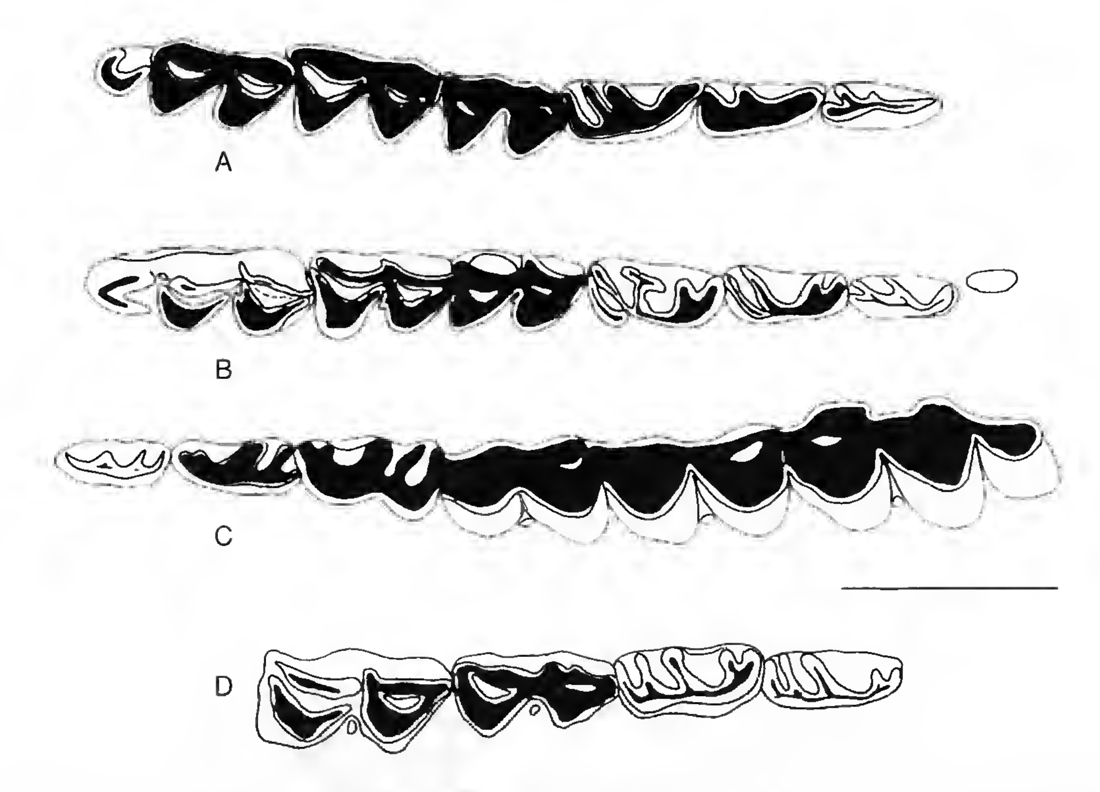


FIG. 3. — Occlusal view of the lower dentition of fossil ruminants from the Sperrgebiet, southern Namibia; **A**, right m3-p2 of *Sperrgebietomeryx wardi* n. gen., n. sp. (EF 37'93), from Elisabethfeld; **B**, right m3-p2 and alveolus of p1, *Propalaeoryx austroafricanus* Stromer (EF 3'93), from Elisabethfeld; **C**, left m3-p2 of *Orangemeryx hendeyi* (AD 1521), from Arrisdrift; **D**, left m2-p3 of *Orangemeryx hendeyi* n. gen., n. sp. (AD 654'94), from Arrisdrift. Scale bar: 20 mm.

HOLOTYPE. — EF 37'93, skull, mandible and associated atlas, with parts of the vertebral column and hind limbs (Figs 2, 3A, 4, 5, 10F-H), housed in the Museum of the Geological Survey of Namibia, Windhoek.

TYPE LOCALITY AND AGE. — Elisabethfeld, Namibia. Early Miocene.

ETYMOLOGY. — *Sperrgebiet*, German name for the "forbidden territory" on account of this name applied to the Diamond Area of southern Namibia; *meryx*, Greek for deer. The species name honours geologist Dr John Ward who found the holotype.

DIAGNOSIS. — Medium-sized giraffoids, premolar series long and gracile. Lower p4 with simple metaconid, directed posteriorly, anterior wing without bifurcation. P2 and p2 nearly the same size as P3 and p3.

DIFFERENTIAL DIAGNOSIS. — *Sperrgebietomeryx* differs from *Propalaeoryx austroafricanus* by its smaller size, by the more primitive morphology of the p4 and P4, and the loss of p1. It differs from *Walangania africana* (Whitworth 1958) by its larger size, the more gracile premolars and the more primitive construction of the p4 and P4. It differs from *Prolibytherium* Arambourg, 1961, Giraffidae and Climacoceratinae by the absence of cranial protuberances which are present in the latter three groups.

DESCRIPTION

The skull (Figs 3-4) is well preserved, although eroded on the anterior part of the left side, and slightly crushed dorsoventrally. In ventral view the skull presents a clearly primitive morphology, comparable to that of *Dremotherium* (Sigogneau 1968). The auditory region is of primitive type, with the styloid process located between the mastoid process and the tympanic bulla, the latter being moderately inflated, while the external auditory meatus is prominent and almost circular. The basioccipital is relatively wide, with strong posterior and anterior tubercles for muscle insertions. The width of the insertion zone for the

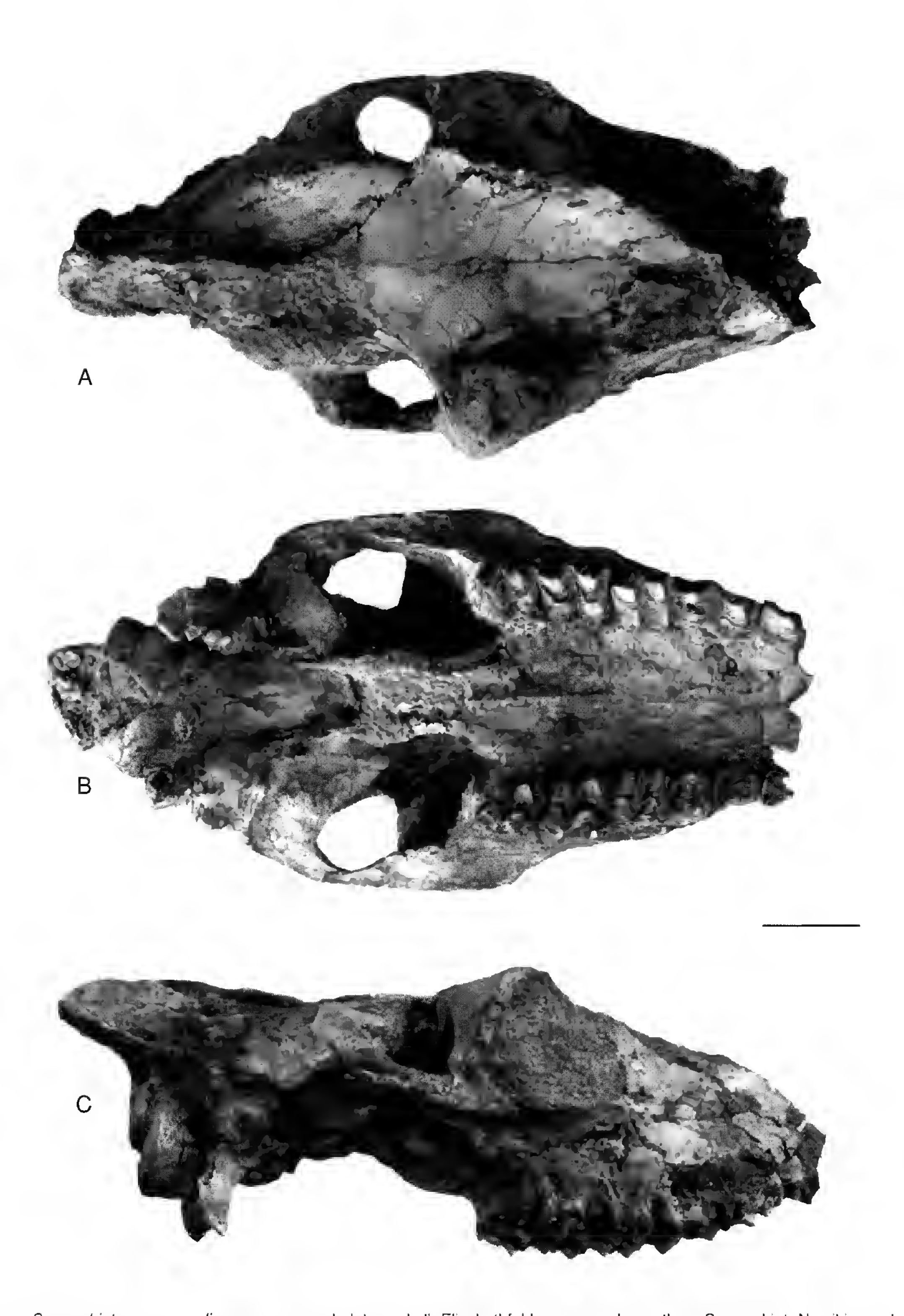


FIG. 4. — *Sperrgebietomeryx wardi*, n. gen., n. sp., holotype skull, Elisabethfeld green sands, northern Sperrgebiet, Namibia, early Miocene; **A**, dorsal view; **B**, ventral view; **C**, right lateral view. Scale bar: 20 mm.

TABLE 1. — Measurements (length, width, in mm) of the upper dentition of *Sperrgebietomeryx wardi* n. gen., n. sp. from Elisabethfeld (EF 37'93), *Propalaeoryx austroafricanus* from Elisabethfeld (EF 4'93) and *Orangemeryx hendeyi* n. gen., n. sp. from Arrisdrift.

	S. wardi		*P. austroafricanus*			*O. hendeyi*		
	r EF 37'93	l	EF 4'93	EF200'93	EF201'93	AD273	AD283'94	AD334'95
LMM-PP	68.0	–						
LMM	39.5	38.2	41.5			63.0		
LPP	31.0	–	–					
LM3	13.5	13.0	14.0			21.6		
WM3	12.8	12.3	–			18.2		
LM2	13.6	13.5	15.1			21.4		
WM2	15.5	15.2	–			21.9		
LM1	13.5	12.2	13.0			21.0		
WM1	13.0	12.2	–			20.0		
LP4	10.0	9.5	10.5	11.4		13.1		
WP4	10.0	10.5	–	10.3		15.9		
LP3	10.0	10.7					11.5	
WP3	9.5	9.2					13.2	
LP2	10.4	–			12.5			14.1
LP2	8.9	–			–			11.8

masseter muscles is remarkable, and reveals their strength. In dorsal view, the width of the frontals, the strength and height of the sagittal crest and of the nuchal crest are all notable features of the skull. The zygomatic process of the frontal is very prominent. The frontals are relatively wide, although they appear wider on account of the dorsoventral compression that affects the skull. There is no lacrimal fossa, and there may have been an ethmoidal fenestra although the preservation of this part does not allow of certainty in this matter. The external occipital protuberance is very strong and projects posteriorly. The supraoccipital has a well-marked crest.

Upper dentition (Table 1, Fig. 4B)
Molars with strong parastyles and mesostyles; in the M3 the metastyle is also strong. The internal

TABLE 2. — Measurements (length, width, in mm) of the lower dentition of *Sperrgebietomeryx wardi* n. gen., n. sp. from Elisabethfeld (EF 37'93), cf. *Strogulognathus* (Stromer 1926); *Propalaeoryx austroafricanus* from Elisabethfeld (EF 3'93) and Langental (1926-507, holotype), cf. *Strogulognathus sansaniensis* from Langental (Stromer 1926) and *Orangemeryx hendeyi* n. gen., n. sp. from Arrisdrift.

	S. wardi	cf. *Strogulog.*	*P. austroafricanus*		*O. hendeyi*		
	EF 37'93	I	EF 3'93	1926-507	N	OR	M
LMM-PP	75.0		82.0	90.6	9	95.0-109.0	100.6
LMM	44.0		48.2	52.8	12	58.0-65.5	62.1
LPP	32.0		34.9	37.0	13	34.6-45.5	38.6
Lm3	18.5	18.0	21.5	21.2	14	24.2-29.0	26.7
Wm3	8.0	8.0	8.5	9.0	13	9.5-11.5	10.6
Lm2	13.6	13.0	13.0	15.5	17	17.0-21.5	20.2
Wm2	8.9	9.0	7.9	9.4	17	10.2-13.0	11.9
Lm1	12.5		12.5	14.8	16	15.2-20.5	16.7
Wm1	7.9		7.0	8.8	16	9.3-12.0	10.5
Lp4	12.2		12.5	13.0	18	12.5-15.5	14.5
Wp4	5.7		7.7	6.5	18	8.0-10.0	8.9
Lp3	10.9		12.0	12.4	13	11.3-15.1	14.1
Wp3	5.5		6.5	–	13	6.0-8.2	7.3
Lp2	9.5		10.2	10.5	8	9.0-12.5	9.9
Wp2	4.1		5.0	4.3	8	4.0-5.7	4.8
Lp1			5.0	6.0			

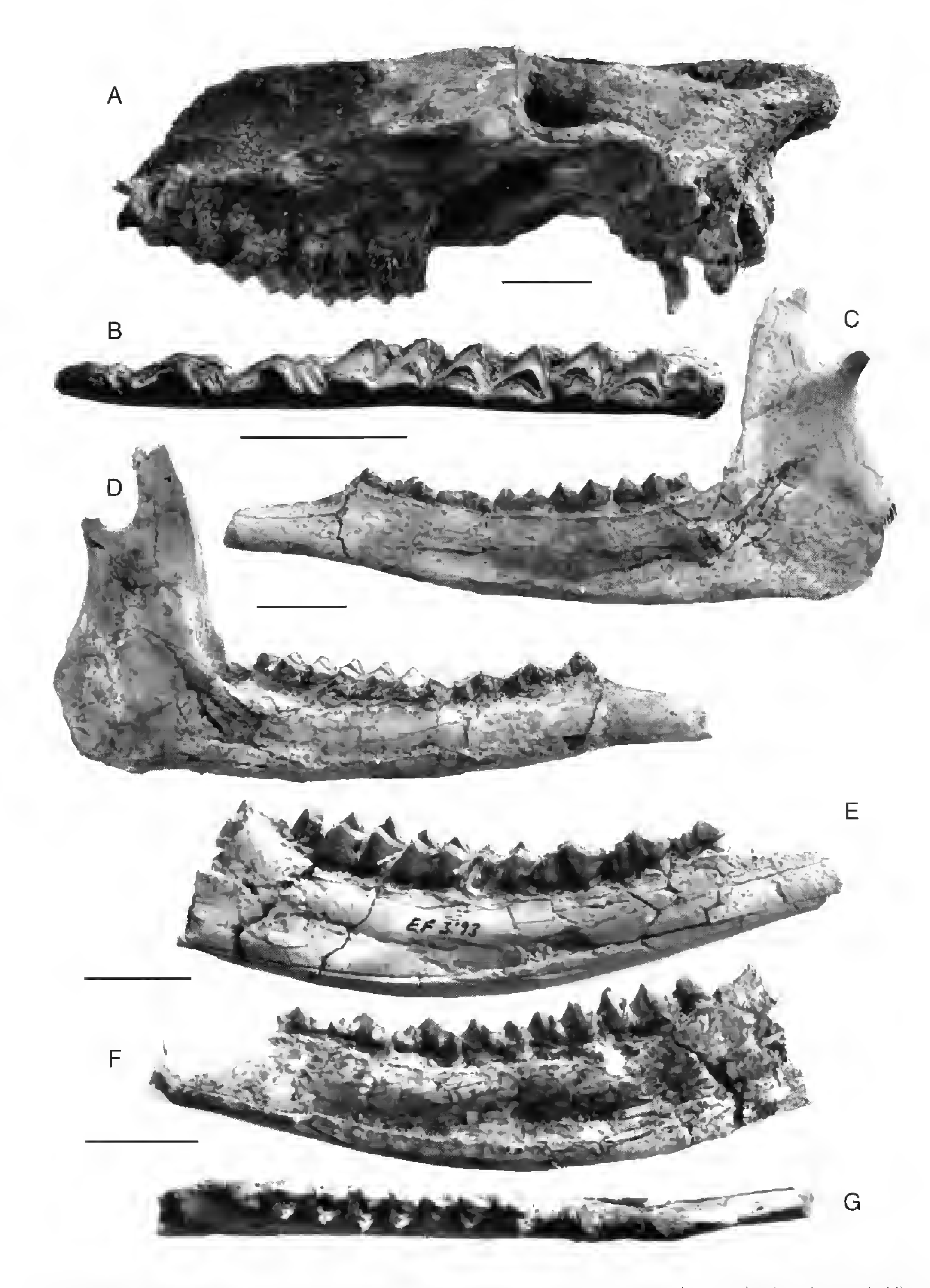


FIG. 5. — **A-D**, *Sperrgebietomeryx wardi* n. gen., n. sp., Elisabethfeld green sands, northern Sperrgebiet, Namibia, early Miocene; **A**, holotype skull in left lateral view; **B-D**, right mandible; **B**, occlusal view of cheek dentition; **C**, lingual view; **D**, buccal view; **E-G**, *Propalaeoryx austroafricanus*, Stromer, Elisabethfeld red silts, northern Sperrgebiet, Namibia, early Miocene, right mandible; **E**, buccal view; **F**, lingual view; **G**, occlusal view. Scale bars: 20 mm.

lobes fuse late with each other, the interlobular column is small. M2 is larger than the other two molars, which are approximately the same size. The premolars are long, including the P4, which possesses a strong anterior style with a cingulum round the protocone. P3 and P2 also possess a strong anterior style and a well-defined anterior lobe [close morphologically to the premolars of Boselaphini (Bovidae)].

Lower dentition (Table 2, Fig. 5B-D)
The stage of wear prevents much being observed, especially in the molars. The third lobe of m3 is relatively small. The premolars are long and gracile. The close morphological similarity between the premolars is notable, especially between p3 and p4. Both premolars have simple metaconids directed posteriorly and the anterior wing without bifurcation, while the external incision is moderate.

DISCUSSION
The existence of two ruminant species in the early Miocene of the northern part of the Sperrgebiet was noted by Stromer (1926) on the basis of fossils from Langental and Elisabethfeld assigned by him to cf. *Strogulognathus sansaniensis* Filhol, 1870 and *Propalaeoryx austroafricanus* Stromer, 1926, respectively. The dentitions assigned to *Strogulognathus* were slightly smaller than those assigned to *Propalaeoryx austroafricanus*, but were otherwise similar to them, which is why they have subsequently been pooled with those of *P. austroafricanus* (Hamilton & Van Couvering 1976).

Genus *Propalaeoryx* Stromer, 1926

TYPE SPECIES. — *Propalaeoryx austroafricanus* Stromer, 1926.

HOLOTYPE. — 1926-507, mandible.

TYPE LOCALITY. — Elisabethfeld, Namibia.

NEW COLLECTIONS. — Elisabethfeld, Namibia: EF 3'93, right mandible (Table 2, Fig. 5E-G); EF 4'94, fragment of right maxilla with damaged P4-M3; EF 200'93 right P4; EF 2001'93 left P2 (Table 1).

DESCRIPTION
The mandible has lost the ascending ramus and the symphyseal portion. The horizontal ramus is robust and preserves the alveolus for p1 which is uniradiculate. The lower molars possess a moderate paleomeryx fold, most marked in the m1. The metastylid is strong and isolated. The posterior wing of the hypoconid is well separated from the entoconid. The basal pillar is of moderate size. The hypoconulid of the m3 is simple and of moderate size. The p4 presents a bifurcate anterior wing and complex metaconid positioned in front of the protoconid and forming an incipient internal wall. There is a deep vertical incision in the posterior part of the external wall. The p3 is much simpler. It also has a bifurcate anterior wing, but the metaconid is a simple crest directed backwards. The p2 is smaller than p3 with a simple anterior wing. The dimensions (in mm) of the specimen are as follows: molar series 48.2; premolar series (without the p1) 34.9; m3 21.5 × 8.5; m2 13 × 7.9; m1 12.5 × 7; p4 12.5 × 7.7; p3 12 × 6.5; p2 10.2 × 5; p1 (alveolus) 5 × 2.
The maxilla fragment is badly abraded so that the internal lobes of the four teeth P4-M3 have been partly destroyed, so that only the external length of the teeth can be measured, as follows (in mm) : M3 14; M2 15.1; M1 13; P4 10.5. In the three molars the parastyle and mesostyle are well-developed and externally well-defined. In the M3 there is, in addition, a strong metastyle which is also well defined externally and which is united by a basal cingulum to the other styles. The P4 is elongated with strong parastyle and metastyle.
The isolated P4 (11.4 × 10.3 mm) has an external wall similar to that in the specimen described above. The protocone is surrounded by a relatively strong cingulum.
The isolated P2 (length 12.5 mm) is missing its protocone. The parastyle is large and globular. The paracone is well marked externally and is joined to the parastyle by a smooth cingulum which continues to the posterior margin.

DISCUSSION
The Elisabethfeld *Propalaeoryx* mandible differs from that of *Sperrgebietomeryx* by its larger size, the presence of a well-developed p1 and premolars which are more robust and complex. The p4s are particularly different, those of

Propalaeoryx Stromer, 1926, possessing a bifurcate anterior wing, a strong metaconid which forms an incipient lingual wall, and a deep external incision. In all these characters this specimen is close to the holotype mandible of *Propalaeoryx austroafricanus*, although the latter is slightly larger and has a simpler metaconid in its p4. The new jaw from Elisabethfeld has hypsodont molars and, as in the holotype, the palaeomeryx fold is weak, being strongest in the m1.

TABLE 3. — Measurements (in mm) of the postcranial skeleton of *Sperrgebietomeryx wardi* n. gen., n. sp. from Elisabethfeld and *Propalaeoryx austroafricanus* from Elisabethfeld and Langental (Stromer 1926). Abbreviations: **APD**, antero-posterior diameter; **TD**, transversal diameter; **c.c.**, corpus calcanei; **t.c.**, tuber calcanei; **m.**, maleolus; **s.**, sustentaculum.

		S. wardi		**Stromer, 1926**	***P. austroafricanus***
RADIUS	EF 21'94	EF 23'94	EF 24'94	8	EF 41'94
Length	214.0				
Proximal APD	15.9			16.0	17.7
Proximal TD	27.9			28.0	31.5
Distal APD			19.4		
Distal TD		25.6	25.1		

	S. wardi	***P. austroafricanus***
HUMERUS	EF 36'94	EF 22'93
Distal APD	28.0	30.0
Distal TD	28.6	34.1

	S. wardi	**Stromer, 1926**		
SCAPHOID	EF 23'94	10α	10β	10γ
Anterior Height	13.1	13.0	12.5	14.8
APD	17.2	18.5	19.0	20.5

	S. wardi	**Stromer, 1926**
SEMILUNAR	EF 23'94	9
Anterior Height	12.4	12.0
Proximal APD	16.3	
Proximal TD	13.5	14.5

	S. wardi	**Stromer, 1926**
FEMUR	EF 37'93	15
Proximal TD	50.0	52.0
Head APD	22.1	20.0
Head TD	28.1	27.0

		S. wardi	
METACARPAL	EF 35'93	EF 23'94	EF 24'94
Length	207.2		205.0
Proximal APD	17.3		17.8
Proximal TD	21.4	22.1	
Distal TD	23.8		

	S. wardi	**Stromer, 1926**	
TALUS	EF 37'93	18a	18b-β
Lateral Length	31.4	31.0	35.5
Medial Length	29.9		
Lateral APD	18.3		
Distal TD	20.2	19.0	21.2

	S. wardi	***P. austroafricanus***
CALCANEUM	EF 37'93	EF 36'93
Length	70.9	
c.c. Length	49.0	50.3
t.c. APD	18.4	20.2
t.c. TD	17.8	18.4
c.c. APD	18.9	18.3
c.c. TD	8.6	9.9
m. APD	25.9	
s. TD		21.3

	S. wardi	**Stromer,1926**	
TIBIA	EF 37'93	16α	16β
Length	257.0		
Proximal APD	46.0		
Midshaft APD	17.8		
Midshaft TD	20.7		
Distal APD		23.5	24.0
Distal TD	29.0	31.0	30.0

	S.wardi		*P.austroafricanus*	Stromer, 1926
I PHALANX	EF 24'94	EF 27'94	EF 28'94	13α
Length	34.7	39.8	43.5	42.0
Proximal APD	13.7	15.2	16.2	
Proximal TD	12.2	14.3	13.9	13.0
Distal APD	9.4	9.5	9.9	
Distal TD	10.1	12.1	11.5	

	S.wardi	Stromer, 1926
II PHALANX	EF 24'94	13β
Length	20.4	21.5-25.0
Proximal APD	12.0	
Proximal TD	10.2	
Distal APD	10.7	
Distal TD	7.9	7.5-9.0

	S.wardi	
III PHALANX	EF 24'94	EF 34'94
Plantar Length		22.3
Dorsocaudal D	17.4	
Dorsoplantar D		13.7

The upper dentition of *Propalaeoryx austroafricanus* was hitherto unknown, and the attribution of the new Elisabethfeld specimen to this species is based on its discovery locus, its size (larger than *Sperrgebietomeryx*) and its more robust premolars.

POSTCRANIAL SKELETON OF *Sperrgebietomeryx* AND *Propalaeoryx*

Vertebral column

Articulated with the holotype skull of *Sperrgebietomeryx wardi* there was the atlas (Fig. 2) and three cervical vertebrae (the axis, V3 and V4). The atlas is notable for its elongation, being almost as long as it is wide, and in this respect resembles the atlas of several antelopes such as *Gazella dama* Pallas, 1766. The margins of the wings are virtually parallel and straight. The axis and the other vertebrae are poorly preserved, only V3 being complete and revealing that it too was elongated.

Limb bones

Elisabethfeld has yielded some thirty ruminant limb bones, in addition to the partial skeleton found with the holotype skull and mandible of *Sperrgebietomeryx wardi*. Many of the specimens have been sand-blasted and some are broken, so it is often difficult to assign them taxonomically. Because of the uncertainty in identifying to which species the bones belong we describe the specimens together, but suspect that the larger specimens belong to *Propalaeoryx austroafricanus* Stromer, 1926, while the others probably represent *S. wardi* (Table 3).

Specimens EF 22'93, a distal humerus (Fig. 10E), EF 41'94, a proximal radio-ulna, EF 36'93, the body of a calcaneum, and EF 28'94, a first phalanx, are assigned provisionally to *P. austroafricanus*.

The following specimens are assigned to *S. wardi*: EF 36'94 and EF 22'94, distal humeral epiphyses; EF 21'94, a complete radius; EF 23'94, articulated juvenile radial epiphysis, carpus and proximal end of metacarpal; EF 24'94, articulated radius, metacarpal and phalanges; EF 35'93, complete metacarpal; EF 37'93, proximal half of a femur, tibia, talus, calcaneum found with the holotype skull, mandible and atlas; EF 27'94, first phalanx; EF 34'94, third phalanx.

Humerus

S. wardi has the radial fossa limited by a tuberosity which reaches the lateral epicondyle, and is very large because the capitulum has a moderate vertical development and proximally does not ascend greatly, while distally it stays at the same level as the trochlear groove. The humerus of *P. austroafricanus* is similar but it is slightly wider, has a medial condyle which is less well-developed proximodistally, and has very strong relief in the medial epicondyle



FIG. 6. — *Orangemeryx hendeyi* n. gen., n. sp., frontal apophyses from Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**-**C**, holotype frontal with base of left apophysis (AD 595'94); **A**, medial view; **B**, frontal view; **C**, lateral view; **D**, **E**, lower part of apophysis lateral views (AD 130); **F**, mid-part of apophysis with base of bifurcation towards top of frame (AD 131). Scale bars: 20 mm.

Radius
The proximal epiphysis is the same in the two species, but in *P. austroafricanus* it is slightly bigger and the lateral tuberosity is stronger. The diaphysis in EF 21'94 (Fig. 10G) is gracile, and the articular facets of the distal epiphysis in all the specimens have the typical morphology of early Miocene ruminants: that of the pyramidal is small and horizontal, whereas that for the scaphoid is larger and more elevated than that of the semilunar and there is a platform for the ulna contact.

Carpus
The material is articulated making it difficult to observe all the morphological details (Fig. 10F). The semilunar is subquadrangular and the distal lateral facet is much wider than the medial one, also its morphology and measurements are identical to those of cf. *Strogulognathus sansaniensis* Filhol, 1870, cited by Stromer (1926, pl. 40, fig. 4).

Metacarpal
This bone is long and gracile (Fig. 10H), the diaphysis having a flat posterior surface, and the proximal extremity being narrow with respect to the antero-posterior diameter. The facet for the magnotrapezoid is very large compared to that for the unciform. The distal pulleys have well-developed keels posteriorly.

Femur
The proximal half is preserved but both trochanters are broken. On the posterior surface, below the lesser trochanter, there is a roughened triangular area delimited by two crests which continue parallel to the length of the diaphysis as in the extant giraffid species *Okapia johnstoni* (Sclater 1901).

Tibia
This bone is also long, gracile and straight. The tibial crest is long, reaching to mid-shaft of the diaphysis. On the posterior surface next to the popliteal line there is another line parallel to it and somewhat shorter, also as in *Okapia*. The medial distal groove is wide and shallow. In distal view the anterior and posterior margins of the epiphysis are markedly concave and the wall which separates the trochlear facets is short antero-posteriorly.

Astragalus
Corresponding to the morphology of the distal tibia, the depression between the two condyles of the proximal end is deep and is also asymmetrical. In the medial condyle there is a strong posterior process, and on the anterior surface on both sides of the fossa there are well-developed stop facets. On the distal end, the lateral condyle is more extensive than the medial one.

Calcaneum
The calcaneum of *Sperrgebietomeryx wardi* has a symmetrical tuber with a wide but short and deep posterior fossa. Its body is straight, the distal lateral groove is smooth and the distal facet for the astragalus is oblique. In the calcaneum of *P. austroafricanus* the tuber is asymmetric and more strongly developed, both transversely and antero-posteriorly. The rugose postero-medial area is also more developed.

Metatarsal
The only specimen in the collection is a distal juvenile fragment (EF 25'94) that shows an open anterior groove. Its attribution to *Sperrgebietomeryx wardi* is based on its size.

Subfamily CLIMACOCERATINAE Hamilton, 1978

DIAGNOSIS. — Climacoceratidae with frontal protuberances of apophyseal nature (Bubenik 1990). Dentition hypsodont. Premolar row shortened. Lower molars without palaeomeryx fold. Upper molars with external fusion of the lingual and buccal lobes.

Orangemeryx n. gen.

TYPE SPECIES. — *Orangemeryx hendeyi* n. sp.

DIAGNOSIS. — As for the type species.

Orangemeryx hendeyi n. sp.

Climacoceras sp. – Hendey 1978.

HOLOTYPE. — AD 595'94, left frontal fragment with



FIG. 7. — *Orangemeryx hendeyi* n. gen., n. sp., frontal apophyses from Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**, apophyseal point (AD 1798); **B**, apophyseal point (AD 1177); **C-F**, apophysis with trifurcate tip (AD 594'94); **C-E**, various views; **F**, dorsal view; **G**, **H**, bifurcate apophyseal tip, lateral views (AD 649 + 763). Scale bars: 20 mm.

apophysis, housed at the Geological Survey of Namibia, Windhoek (Fig. 6A-C).

LOCALITY AND AGE. — Arrisdrift (southern Sperrgebiet, Namibia), early middle Miocene, approximately equivalent to mammal zone MN4 of the European scale (De Bruijn *et al.* 1992). Pickford (1994) estimates the age of the site to be ca 17.5 Ma.

ETYMOLOGY. — For the Orange River which is the border between Namibia and South Africa and *meryx* the Greek word for deer. The species is dedicated to palaeontologist Dr Q. B. Hendey.

DIAGNOSIS. — Climacoceratinae with elongated slightly compressed truncate conical supraorbital apophyses, ornamented at the base with rounded tubercles with bifurcated or trifurcated upper termination (two or three points).

DIFFERENTIAL DIAGNOSIS. — *Orangemeryx* differs markedly from the other two genera of climacoceratines by the morphology of its apophyses, which are short with a wide base which diminishes towards the apex, giving the apophysis an elongated, slightly compressed truncated conical aspect, different from the cylindrical form that occurs in *Nyanzameryx* Thomas, 1984 and *Climacoceras* MacInnes, 1936.

DESCRIPTION

Holotype: The frontal bone is very thick and strongly vascularised but not enough to be called pneumatised. The supraorbital foramen is well-defined and externally continues to the apophysis following a smooth canal. The postcornual fossa is deep and continues posteriorly as a wide but not very deep, well-demarcated groove. The apophysis is in the form of an elongated compressed cone, with the base wide and diminishing in section towards the apex, while the base is compressed transvetsally (antero-posterior diameter = 44.5 mm, transversal diameter = 29.0 mm), whereas towards the apex the section is almost circular. There is a smooth anterior keel, accompanied by a small protuberance, the posterior margin is rounded with a weaker but more extensive protuberance. The apex is broken, so that it is possible to observe that the wall of the apophysis is thick and the central part vascularised (Fig. 8E).

Other specimens such as AD 130 (Fig. 6D-E), AD 250, AD 483, AD 596'94 (Fig. 8A-E) and AD 132 (Fig. 8F-G), are similar to the holotype, even though there is a certain amount of variability in the shape and size of the protuberances of the apophyses. At the base of the apophysis in AD 596'94 (Fig. 6A-E), there are shallow sinuous canals indicating the courses followed by blood vessels, which suggest that the apophyses were covered in skin. AD 131 (Fig. 6F) is the apical and medial part of an apophysis which possesses a lateral protuberance similar to those mentioned above. This specimen indicates that the apophysis bifurcates towards the apex, also evidenced by the surface ornamentation in the form of a Y. Other specimens indicate a more complex apex than this fossil, one of which AD 648+763 (Fig. 7G), illustrated by Hendey (1978) shows a tip with two different sized points, while another AD 594'94 (Fig. 7C-F) is trifurcate with three approximately similar sized points. Fragments of apophyses such as AD 129 (figured by Hendey 1978) or AD 1798 (Fig. 7A), AD 1177 (Fig. 7B), AD 658'94 and AD 659'94, are probably best interpreted as points at the apex of the apophysis.

A specimen of skull (AD 652'94, Fig. 9B-D) comprises the frontal with the base of the apophysis and part of the parietal back to the union of the temporal lines, where they begin to form the sagittal crest. There is a strong, abrupt change in slope between the parietal and the frontal, while between and anterior to the apophyses there is a deep, rounded depression. In the base of the right apophysis there is a deep, strong postcornual fossa similar to that observed in the holotype, which continues distally as a canal to connect with the temporal line. The temporal lines are well-marked, swelling towards the base of the apophyses, and posteriorly they unite to form a visible thickening, which in the broken surface has a subtriangular section. There was probably a strong development of the nuchal crest. The frontals are very thick and the bone is well vascularised, in particular the large supraorbital foramen which expands into the roof of the orbit. The bases of the apophyses are not pneumatized, and in the right one the long wide voluminous base can be observed, while in the left one, which is more broken, the subtriangular transversal section can be seen to be similar to that in AD 596'94. This cranial fragment is

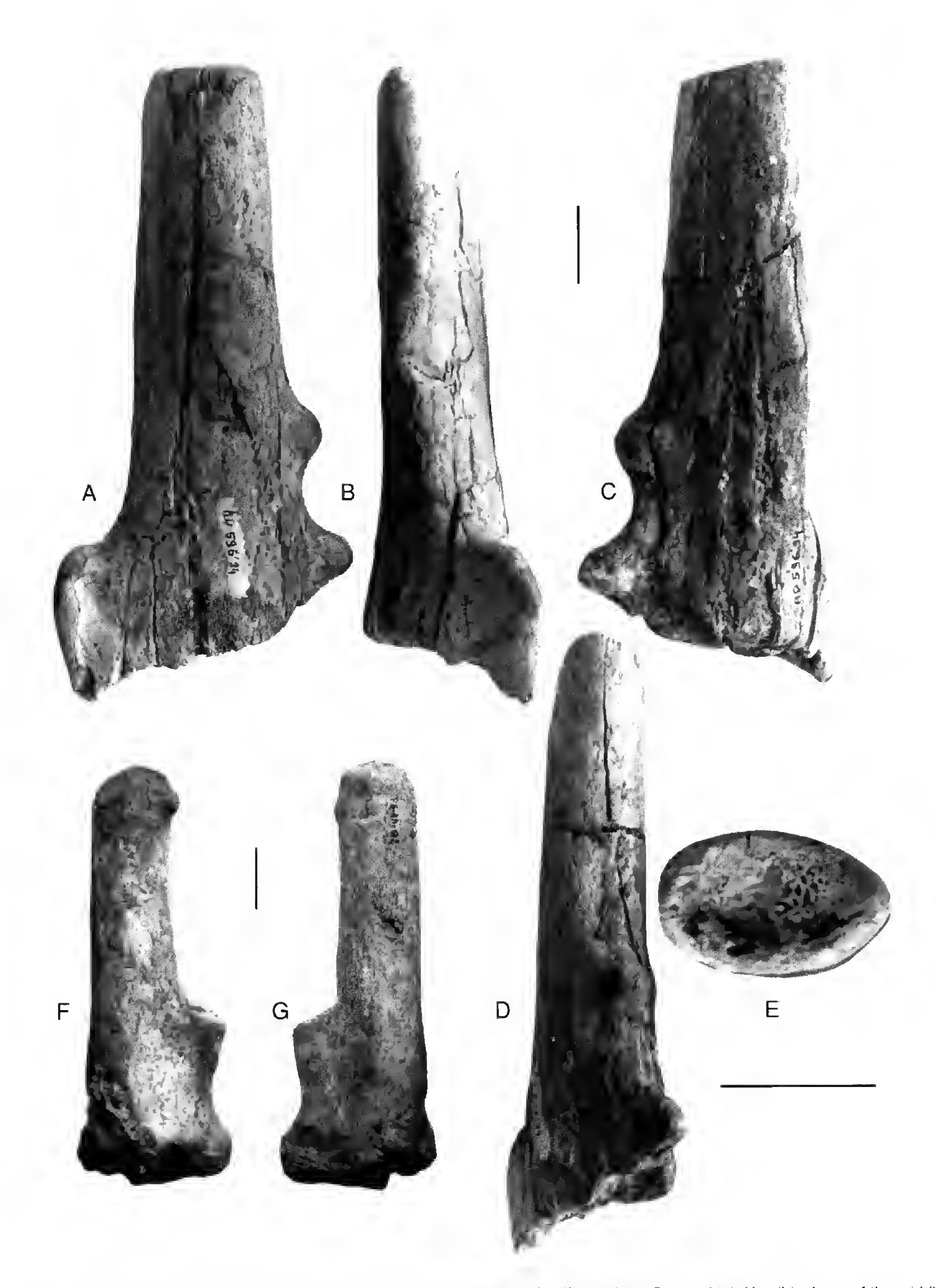


FIG. 8. — *Orangemeryx hendeyi* n. gen., n. sp., frontal apophyses from Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A-E**, left apophysis (AD 596'94); **A**, medial view; **B**, posterior view; **C**, lateral view; **D**, anterior view; **E**, transversal cross section; **F**, **G**, base of apophysis, two views (AD 132). Scale bars: 20 mm.

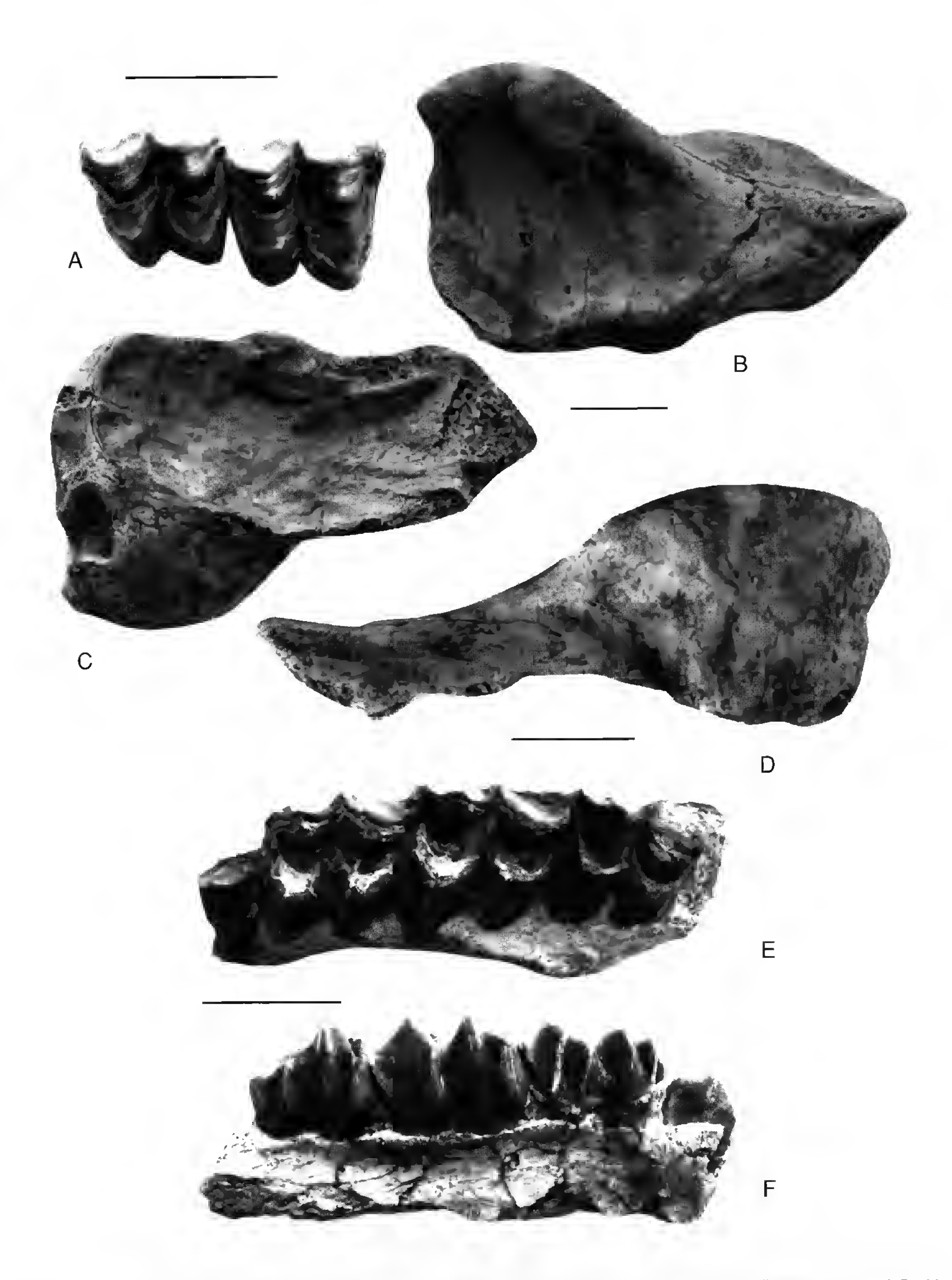


FIG. 9. — *Orangemeryx hendeyi* n. gen., n. sp., Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**, left D4-M1 in occlusal view (AD 624); **B**-**D**, cranial fragment (AD 652'94); **B**, dorsal view; **C**, ventral view; **D**, right lateral view; **E**, **F**, left P4-M3 (AD-273); **E**, occlusal view; **F**, buccal view. Scale bars: 20 mm.

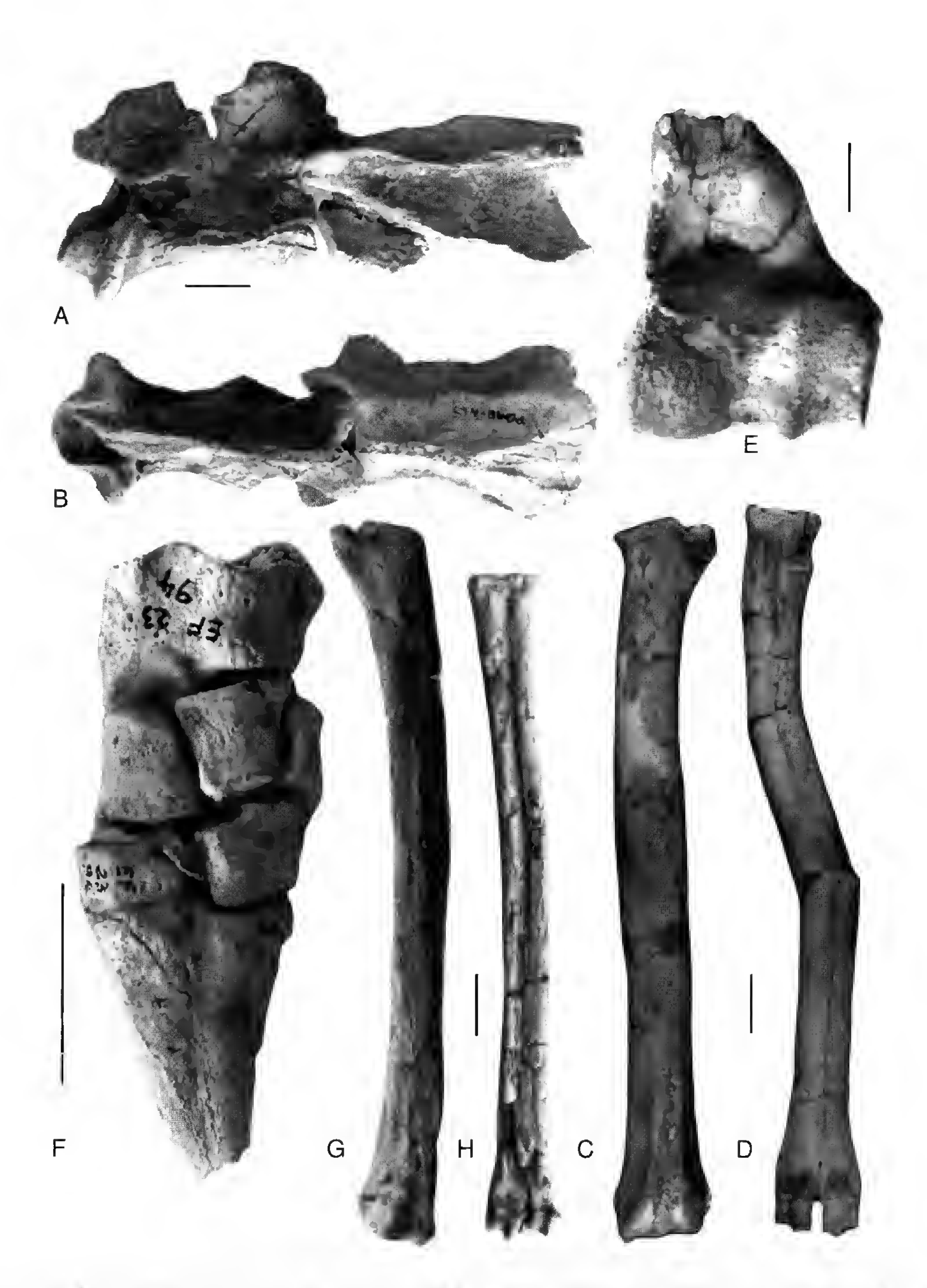


FIG. 10. — **A-D**, *Orangemeryx hendeyi* n. gen., n. sp., Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**, **B**, axis (AD 1549); cervical vertebra V3 (AD 1447); **A**, lateral view; **B**, dorsal view; **C**, left radius, anterior view (AD 00'95); **D**, left metatarsal, anterior view (AD 5'93); **E**. *Propalaeoryx austroafricanus*, Stromer, Elisabethfeld red silts, northern Sperrgebiet, Namibia, early Miocene, left distal humerus, anterior view (EF 22'93); **F-H**, *Sperrgebietomeryx wardi* n. gen., n. sp., Elisabethfeld green sands, northern Sperrgebiet, Namibia, early Miocene; **F**, left juvenile distal radius, carpus, and proximal metacarpal (in anatomical connection), anterior view (EF 23'94); **G**, right radius, anterior view (EF 21'94); **H**, left metacarpal, posterior view (EF 35'93). Scale bars: 20 mm.

useful in providing evidence as to the correct orientation of rhe apophyses in *Orangemeryx*, especially the holotype AD 595'94, in which it was inclined slightly laterally and forwards.

Dentition

The cheek teeth are relatively hypsodont, being similar in many respects to the dentition of other climacoceratids. Lower molars (Table 2, Fig. 3C) possess strong metastylids which projecr laterally. The protoconid and hypoconid are flattened. The hypoconid and protoconid are separated, only uniring when wear is advanced. The hypoconulid of m3 is simple and unicuspidate. The premolars are short. The p4 is variable, always with the anterior wing bifurcate and a strong labial groove, the metaconid varies from being isolated to forming a wall which unites with the metastylid. Incisiform teeth are well represented in the collection, none of which are bilobed. Upper molars (Table 1, Fig. 9A, E, F) have internal lobes separared from each other. The styles are strong, particularly the parastyle and merastyle. The entostyle is weak. Upper premolars are shorr and wide.

Vertebral column

Numerous vertebrae of *Orangemeryx hendeyi* are preserved, some of them in articulation. All in all they possess morphological features typical of modern ruminants. Among the cervical vertebrae there is an axis (AD 1549, Fig. 10A-B) which is relarively complete. It is notably elongated and rhe spinous process is distincrly high and well-developed, which suggests the existence of strong muscularure related ro movements of the head. A further well-preserved cervical vertebra (AD 1447, Fig. 10A, B), like the previous specimen, is elongated.

Limb bones

The sample of limb bones assigned ro *Orangemeryx hendeyi* is very comprehensive, bones of this species being the most common mammal remains at the site (over 220 specimens). In the sample are complete examples of most limb elements, but some of them have been deformed by compaction and several have been damaged by gypsum crystal growth (Table 4, Fig. 10C, D).
The morphology of the limbs is quire generalized, except for their elongation, indicating that *O. hendeyi* was not greatly specialized, retaining much of the aspecr of what we consider to be the basal giraffoid condition. Many of the postcranial elements of these ruminants possess a rather constant morphological pattern, whereas others presenr major variability and appear to be more closely implicated in the processes of adaptation and evolution, even though it is difficult to determine their evolutionary significance. The existence of great variability in the bone size is also noticeable, which should probably be interpreted as a dimorphic pattern. The aim of this section is not to provide a derailed study of each postcranial element, but to provide remarks on the salient features of the limb skeleton of *O. hendeyi*.

Humerus

In the proximal epiphysis (Fig. 11A), the greater and lesser tuberosities are low and there is no intermediate tubercle equivalent to the condition in more modern giraffes. The distal epiphysis is comparable to that of *Sperrgebietomeryx wardi* described above, but the radial fossa is more reduced due to the great proximo-distal development of the capitulum and the medial condyle of the trochlea, a condition which also differentiates it from *Climacoceras gentryi* and *Palaeotragus primaevus*, the humeri of which possess a more "giraffid"-like morphology with the medial condyle low proximally.

Radioulna

The proximal epiphysis of the radius accords with the morphology of the disral humerus, and this bone thus differs in the same way from its counterpart in *P. primaevus*; the lateral facet is higher and the medial one more inclined in *O. hendeyi*. The distal radial epiphysis is similar to that described in *S. wardi*, the diaphysis is quite straight and is antero-posteriorly compressed. The ulna (Fig. 11B-C) is not fused to the radius. Its tuber olecrani possesses high lateral and medial crests, between which is a deep valley, similar to a specimen of *Climacoceras gentryi* Hamilton, 1978, from Ngorora, Kenya.

Carpus

The scaphoid rerains the distal posterior facet

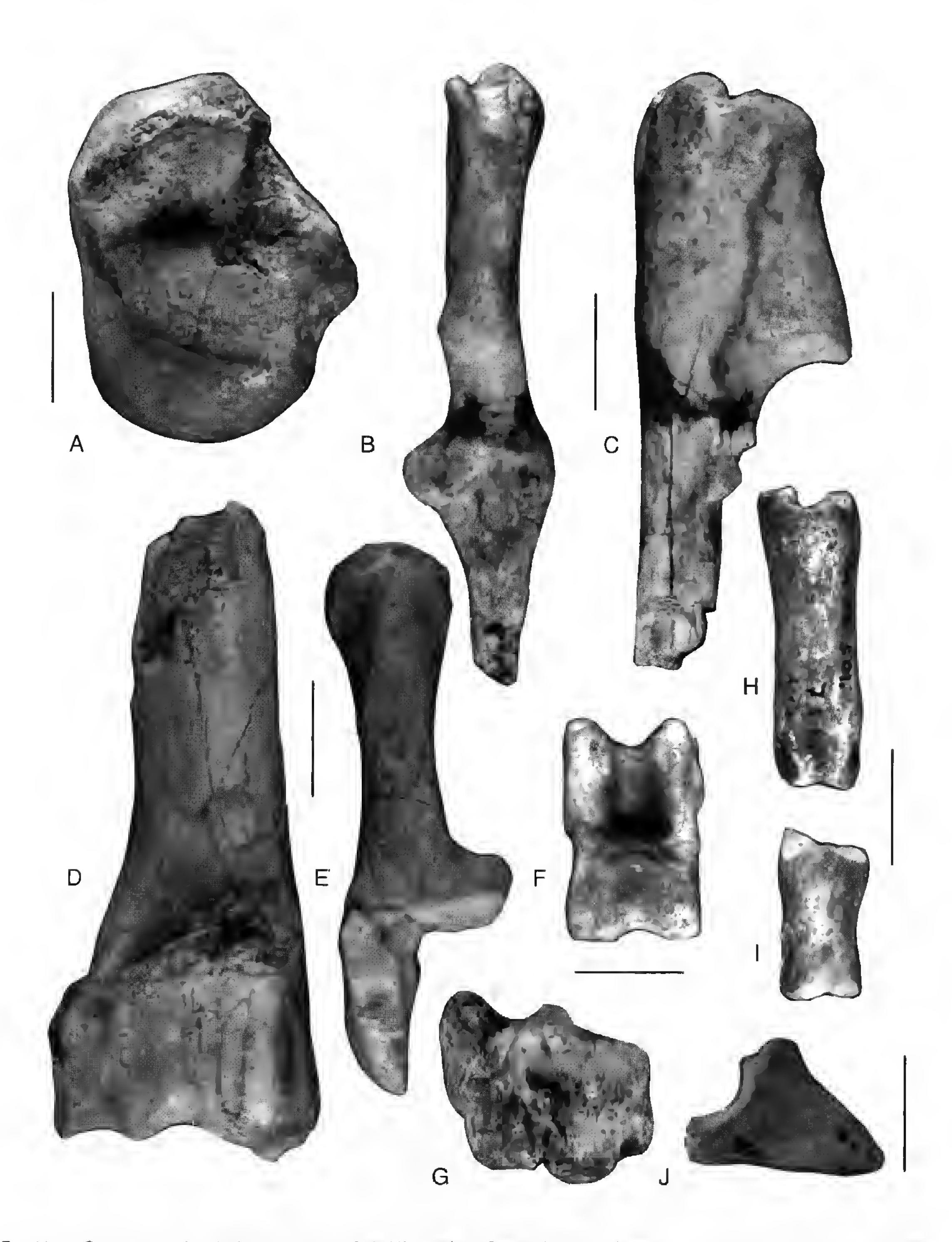


FIG. 11. — *Orangemeryx hendeyi* n. gen., n. sp., Arrisdrift, southern Sperrgebiet, Namibia, base of the middle Miocene; **A**, left proximal humerus, proximal view (AD 3380); **B-C**, right proximal ulna (AD 00'95); **B**, anterior view; **C**, lateral view; **D**,right distal humerus, anterior view (AD 1915) ; **E**, right calcaneum, anterior view (AD 747); **F**, right talus, anterior view (AD 613'94); **G**, right navicular cuboid, posterior view (AD 317'95); **H**, I Phalanx, anterior view (AD 501); **I**, II Phalanx, anterior view (AD 469); **J**, III Phalanx, lateral view (AD 896). Scale bars: 20 mm.

TABLE 4. — Measurements (in mm) of the postcranial skeleton of *Orangemeryx hendeyi* n. gen., n. sp. from Arrisdrift. Abbreviations: **APD**, antero-posterior diameter; **TD**, transversal diameter; **c.c.**, corpus calcanei; **t.c.**, tuber calcanei; **m.**, maleolus; **s.**, sustentaculum.

	N	OR	M
Humerus			
Length	1		209.5
Proximal APD	3	64.0-71.2	68.0
Proximal TD	1		54.8
Distal APD	6	41.8-48.6	45.2
Distal TD	6	44.6-51.8	47.5
Radius			
Length	9	254.0-287.0	268.0
Proximal APD	10	20.4-26.8	23.8
Proximal TD	10	37.0-46.8	42.1
Midshaft APD	9	14.1-22.3	18.1
Midshaft TD	9	23.0-33.4	28.2
Distal APD	12	23.7-32.9	28.6
Distal TD	13	34.0-46.5	39.5
Ulna			
Olecranon Length	4	49.7-61.0	54.6
Tuber o. APD	4	30.1-37.4	33.6
Tuber o. TD	1		15.2
Pro. anc. APD	6	32.6-45.6	39.0
Proc. anc. TD	9	11.3-14.4	12.7
Scaphoid			
Anterior Height	6	17.4-21.6	19.5
APD	6	24.3-28.5	26.3
Anterior TD	5	12.3-14.6	13.8
Semilunar			
Maximal Height	6	16.1-20.3	18.6
APD	5	24.0-27.9	25.7
Proximal TD	5	14.4-18.6	16.1
Unciform			
Maximal Height	4	12.2-15.2	14.2
APD	4	20.0-24.0	22.3
Proximal TD	4	13.0-17.2	14.9
Metacarpal			
Length	7	242.0-275.0	263.0
Proximal APD	9	21.0-27.4	23.2
Proximal TD	10	29.4-38.0	32.5
Distal APD	8	21.6-26.4	24.1
Distal TD	10	32.0-39.3	35.8
Talus			
Lateral Length	9	38.5-46.3	42.3
Medial Length	9	36.2-44.0	40.7
Lateral APD	10	19.7-27.5	23.0
Medial APD	8	21.5-25.0	24.1
Distal TD	9	22.5-28.8	25.8
Calcaneum			
Length	7	94.0-106.0	100.2
c.c. Length	9	61.0-75.4	67.9
t.c. APD	8	23.1-27.7	25.9
t.c. TD	8	20.1-23.2	21.6
m. APD	6	32.0-39.5	36.2
s. TD	6	26.6-30.2	28.2
Navicular-cuboid			
Anterior Height	8	19.4-25.5	21.7
Posterior Height	5	25.1-29.0	27.2
Maximal APD	7	34.2-40.0	36.2
Maximal TD	8	31.4-36.6	33.6
Metatarsal			
Length	6	252.0-280.0	266.0
Proximal APD	18	29.0-40.0	32.1
Proximal TD	18	26.2-33.0	28.7
Distal APD	10	19.2-25.3	22.0
Distal TD	10	29.1-37.5	33.2
I Phalanx			
Length	13	46.5-57.4	51.6
Proximal APD	12	18.9-22.6	21.0
Proximal TD	13	15.1-19.3	17.3
Distal APD	14	10.5-15.0	13.3
Distal TD	15	12.5-15.8	14.5
I			
I Phalanx			
Length	8	26.5-30.5	28.4
Proximal APD	8	17.1-21.0	19.5
Proximal TD	9	13.0-16.0	14.5
Distal APD	9	14.3-17.6	16.4
Distal TD	9	10.2-14.4	12.0
III Phalanx			
Plantar Length	8	30.1-36.6	33.6
Dorsocaudal D	5	22.7-28.0	24.8
Maximal TD	9	11.7-14.8	12.9

Magnotrapezoid	AD501'95	PQAD2574	AD609'94
Anterior Height	14.8	14.6	
APD	23.8	21.8	19.3
Anterior TD	19.2	16.8	15.0
Posterior TD	18.5	15.3	16.3

Tibia	PQAD2292	PQAD1100	PQAD42
Length	360.0	350.0	317.0
Proximal APD	71.1		
Proximal TD	64.5		59.2
Distal APD	32.1	29.4	27.2
Distal TD	39.1	35.6	34.8

which is lost in some fossil giraffids such as *Palaeotragus microdon* (Koken, 1885), *Samotherium sinensis* (Schlosser, 1903), *Decennatherium pachecoi* Crusafont-Pairo, 1952, and *Sivatherium hendeyi* Harris, 1976, but which is still present in the two extant giraffids (*Giraffa camelopardalis* Linneaus, 1758 and *Okapia johnstoni*). In the semilunar, the distal lateral facet is somewhat wider than the medial one. The magnotrapezoid, which is similar to that of *Palaeotragus primaevus* Churcher, 1970, has a concave posterior margin and begins to develop a posterior keel between the facets for the semilunar and the scaphoid. In the unciform, the semilunar facet is particularly elongated in a posterior sense, characters which it shares with other giraffids.

Tarsus (Fig. 11E-G)
The astragalus is plesiomorphic. It is similar to that of *P. primaevus* but has a weakly expressed posterior process in the medial proximal condyle. There is no strong development of the proximal lateral condyle as occurs in *Climacoceras gentryi*, and the distal trochlea has more or less symmetrical condyles. In posterior view, the navicular cuboid shows a very strong medial crest distally which diminishes to nothing at the proximal zone. It has a fossa in a very lateral position, unlike in *P. primaevus*, *Giraffa* and *Okapia*.

Metatarsal
The proximal epiphysis of the metatarsal has similar morphology to that of *Andegameryx andegaviensis* Ginsburg *et al.*, 1994, and the anterior groove is open distally.
The metacarpal, pelvis, tibia and calcaneum all have a generalized morphology similar to that of *P. primaevus*. However, the scapula of *O. hendeyi* has a less-developed supraglenoid tubercle than that of *Palaeotragus primaevus* whereas its coracoid apophysis is more reduced than it is in the latter species.

DISCUSSION
Orangemeryx shares with other climacoceratines the same morphological pattern of the dentition and the possession of complex supraorbital apophyses. In *Nyanzameryx pickfordi* Thomas, 1984, and *Orangemeryx* the frontal apophyses are ornamented at their bases with rounded protuberances which do not project far enough to form lateral points. In contrast, in *Climacoceras africanus* MacInnes, 1936, and especially in *C. gentryi* Hamilton, 1978, the points are considerably elongated, imparting a deer-like morphology to the apophyses. The morphology of the apophyses permits us to separate the various species into two groups : one comprising the two species of *Climacoceras* plus *Nyanzameryx* Thomas, 1984, the other consisting of *Orangemeryx*.

PHYLOGENETIC RELATIONS

The relationships between these two groups, now considered to be subfamilies of the family Climacoceratidae (= Climacoceridae of Hamilton, 1978), is based on the fact that they share the same morphological pattern of the dentition and the incipient elongation of the neck and the limbs. The presence of elongated cervical vertebrae, including the atlas, was already noted in *Climacoceras gentryi* by Hamilton (1978), the atlas of which is proportionally longer than it is in *Palaeotragus primaevus* and *Samotherium africanus* Churcher, 1970. Even though no atlas of *Orangemeryx hendeyi* has been found, comparison between the axes of this species and that described by Churcher (1970) for *Palaeotragus primaevus* is suggestive in this respect, and indicates to us that this new genus also possessed a long neck.
The new fossil material described here tends to confirm this relationship because *Sperrgebietomeryx*, *Orangemeryx* and *Climacoceras* (*C. gentryi*) share elongated cervical vertebrae, including the atlas, a character which indicates a notable specialization towards feeding from high food sources. In the forms of which the postcranial skeleton is known, it is possible to confirm that the extremities are clearly elongated. The cladogram (Fig. 12) summarizes the phylogenetic relationships between the described forms, considering *Andegameryx* Ginsburg *et al.*, 1994, to be the outgroup.
The family Climacoceratidae has previously been placed close to the giraffes on the basis of the presence of a bilobed lower canine in *Climaco-*

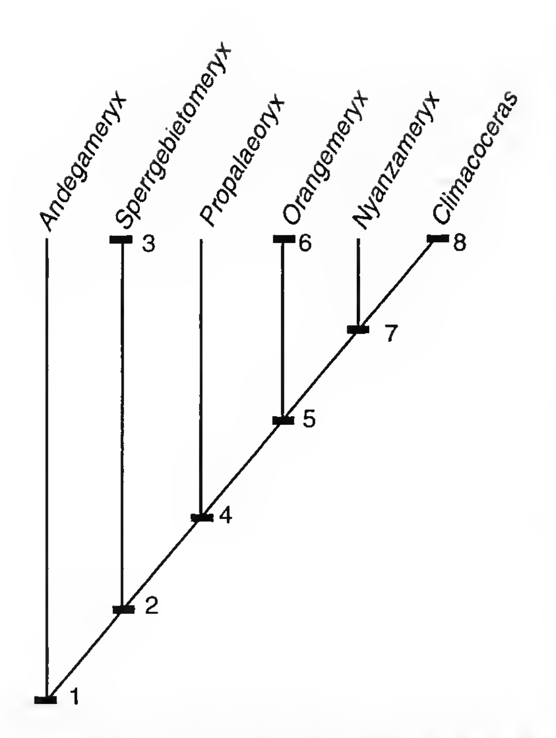


Fig. 12. — Phylogenetic relationships of *Sperrgebietomeryx* n. gen. *Propalaeoryx* Stromer and *Orangemeryx* n. gen. to other giraffoids. Nodes: **1**, (primitive characters) dentition moderately hypsodont; upper and lower premolar series long; premolars elongated and thus gracile; lower molars with strong stylids; third lobe of m3 simple; hypoconid isolated, a consequence of its clear separation from the entoconid and the anterior lobe; the p4 has a simple metaconid, directed posteriorly, anterior wing simple, its morphology differing little from that of the p3; the p1 is present with two strong roots; upper premolars long, P2 and P3 with well-defined anterior lobes; upper molars with strong styles and late union of the internal lobes to the ectoloph; appendicular skeleton gracile, with a tendency to elongation of the elements; **2**, cervical vertebrae, including the atlas, elongated; **3**, loss of p1; **4**, hypsodont dentition. The p4 with metaconid disposed more transversally, with a tendency to turn anteriorly, anterior wing bifurcate (and thus very different from p3), tendency towards flattening of the internal wall of the lower molars; **5**, presence of supraorbital apophyses with protuberant ornamentations at the base, with a bifurcate termination; loss of p1, **6**, apophyses with elongated slightly compressed conical morphology below the bifurcation; **7**, apophyses elongated and cylindrical; **8**, apophyses with well-defined points perpendicular to the long axis of the apophysis (*C. africanus*); apophyses complex, ramified as in some cervids (*C. gentryi*).

ceras gentryi from Fort Ternan (Hamilton 1978), but the presence of this character is not certain, as was noted by Churcher (1990). At Arrisdrift, there are at least sixteen lower incisiform teeth attributed to *Orangemeryx*, none of which is bilobed. If fossil canines and incisors are preserved in the same ratio that occurred in life, then at least four canines should be present in the Arrisdrift sample, in which case the lower canine in *Orangemeryx* consisted of a single lobe. Other authors have advocated this relationship employing for the most part dental characters (Gentry 1994; Gentry & Hooker 1988; Janis & Scott 1987) or have merely considered it as *incertae sedis* within the Giraffoidea (Geraads 1986).

Apparently, the precocious specialisation of the postcranial skeleton separates the Climacoceratidae from the Giraffidae. Nevertheless, primitive giraffes, such as *Zarafa zelteni* Hamilton, 1973, of the early middle Miocene of Gebel Zelten, Libya, also possessed an elongated atlas. However, a deeper study of the postcranial skeleton of the forms involved in this radiation of the Giraffoidea is required before we can confirm that this specialization is a character that permits the inclusion of the Giraffidae and the Climacoceratidae in a monophyletic group.

These new ruminant fossils support the idea expressed by Ginsburg *et al.* (1994) that prior to the appearance of pecorans with frontal protuberances the group would have been strongly diversified, a diversification which affected not only the dentition, but also the postcranial skeleton. We can now determine with some precision the relationships of most of the pecoran forms lacking cranial protuberances which are related at the level of sister groups to pecoran families which do possess such protuberances. Morales *et al.* (1995) described a hornless bovid from Elisabethfeld, a discovery which corroborates this view of ruminant evolution. These findings strongly support the hypothesis that the appearance of cranial protuberances was a biological phenomenon which occurred virtually synchronously (*ca.* 18-17.5 Ma) but independently in various lineages of pecorans (comprising at least the Cervidae, Palaeomerycidae, Giraffoidea and Bovidae). It corroborates the hypothesis of Morales *et al.* (1993) in which the appearance of cranial appendages is considered to have been an organic response to global scale environmental changes which occurred towards the end of the early Miocene.

Acknowledgements

We thank NAMDEB (M. Lain, J. D. Ward, B. Burrell) for access to the Sperrgebiet, Namibia, and for funding and logistical support. Support was also provided by the Mission for Cooperation and Cultural Affairs, Windhoek (Y. Maire, N. Weil), the Collège de France (Y. Coppens), the Muséum national d'Histoire naturelle, Paris (P. Taquet), the Museo Nacional de Ciencias Naturales, Madrid (proyectos PB/95/0113 and PB/95/0114), the Geological Survey of Namibia (B. Hoal) and the Spanish Agency for International Cooperation (AECI). We thank Drs B. Senut, P. Mein, D. Gommery, A.-M. Bacon and J. Ward for help in the field. Research Permission was approved by the National Monuments Council, Namibia (G. Hoveka, A. Vogt). We thank Dr D. Geraads and an anonymous reviewer for their comments on the manuscript.

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Submitted for publication on 10 March 1998;
accepted on 1 December 1998.

Snout proportions in some Eurasian hipparions (Mammalia, Equidae): taxonomic and functional implications

Ann FORSTEN
Finnish Museum of Natural History,
PB 17, FIN-00014 Helsinki (Finland)
ann.forsten@helsinki.fi

Forsten A. 1999. — Snout proportions in some Eurasian hipparions (Mammalia, Equidae): taxonomic and functional implications. *Geodiversitas* 21 (2) : 255-278.

ABSTRACT
In the hipparions, length and breadth of the snout and depth of the nasal opening are not well correlated with one another, nor with the shape and placement of the preorbital fossa, recently considered taxonomically important in these equids. These characters are distributed in a mosaic-like fashion among species, making species differentiation and phylogenetic reconstruction difficult.

KEY WORDS
hipparions,
snout proportions,
phylogeny,
function.

RÉSUMÉ
Les proportions du museau chez quelques hipparions (Mammalia, Equidae) d'Eurasie : implications taxonomiques et fonctionnelles.
Chez les hipparions, la longueur et la largeur du museau ainsi que la profondeur de la fosse préorbitaire ne sont pas clairement correlées entre elles, ni même avec la forme et la position de cette fosse. Pourtant la valeur de ces mesures a été récemment considérée comme ayant une signification taxonomique importante chez ces équidés. Ces caractères suivent une distribution en mosaïque, au sein des différentes espèces considérées, et leur utilité tant pour la différenciation spécifique des hipparions que pour leur analyse phylogénétique est restreinte.

MOTS CLÉS
hipparions,
proportions du museau,
phylogénie,
implications fonctionnelles.

INTRODUCTION

While the preorbital fossa of the cheek has recently been given great weight in hipparion taxonomy, even used for delimiting "supraspecific groups", the proportions and structure of the snout and the nasal opening have largely been ignored. Complete skulls of *Hipparion* de Christol, 1832, are rare. Most often the snout and/or the cranium are broken off, leaving the middle part of the skull with the cheeks, tooth rows and orbits preserved. Thus there is much less data on the snout of *Hipparion* than on the preorbital fossa of the cheek.

The function of the fossa in *Hipparion* is still unsolved, although there are several alternative hypotheses (see discussion in Sefve 1927: 67-78). In recent equids the shallow fossae serve as attachment areas for levator muscles of the upper lip (Ellenberger & Baum 1943; Zhegallo 1978); the very mobile lips function together with the incisors in gathering food. The extension of the nasal opening in *Hipparion* may reflect the development of the nasal diverticulae, in recent equids situated within the nasal opening (Ellenberger & Baum 1943; but see Gregory 1920).

The shape of the snout in fossil and extant herbivores has recently been debated (e.g. Bunnell & Gillingham 1985; Solounias & Moelleken 1993; Dompierre & Churcher 1996; Eisenmann 1998) and there have been attempts to interprete it ecologically. The shape of the snout is believed to be dictated by the mode of feeding. A broad, anteriorly flattened snout is interpreted as indicating grazing or the unselective gathering of food near the ground. A narrow snout, with the incisors in a sharp arc, is interpreted as indicating browsing or the selective gathering of food at different heights (for the illustration of equid snouts of different breadth, see Eisenmann 1998, fig. 5: 1-10).

In an earlier paper, I (Forsten 1983) discussed the variation in the placement and shape of the preorbital fossa in some Old World *Hipparion*. In the present paper I will describe, compare and discuss the snout and the nasal opening. Old World hipparions group into broad- and narrow-snouted taxa, but with many intermediates. There is weak correspondence with groups delimited on the basis of the preorbital fossa. Also snout proportions and nasal opening extension are only weakly correlated. How should these characters be evaluated and weighted taxonomically and phylogenetically?

METHODS

In the upper jaw, snout length was measured as the distance from the prosthion (I1-I1) to the middle of a line uniting the anterior tips of P2 (Gromova 1952, table I, skull measure 18); snout width was measured as the outer distance behind I3-I3 (Gromova's measure 40). The nasal opening is the distance anteriorly from between the premaxillae (not including the upper symphysis) posteriorly to where the nasals and premaxillae/maxillae meet (Gromova's measure 28). Skull length, since seldom measureable, was here substituted by the distance P2-anterior rim of orbit (Gromova's measure 11), which is roughly correlated with basal length.

In the lower jaw snout breadth was measured as the outer distance behind i3-i3 (Gromova 1952: table IV, measure 14) and symphysial length anteriorly from between i1-i1 posteriorly to the symphysial notch (Gromova's measure 11).

Relative snout width is expressed in scatter diagrams, plotting maxillar snout width to snout length and mandibular snout width to symphysial length, respectively. Snout length is related to skull length by plotting it to the distance P2-orbit. Nasal opening length is expressed both as an absolute measure and in relation to the tooth row. The preorbital fossa is discussed in terms as in Forsten (1983). I calculated 95% equiprobability ellipses on the data of *H. schlosseri-dietrichi* from Samos Q1 and Samos without more exact locality data and of *H. moldavicum* Gromova, 1952 from Taraklia and Novoelizavetovka, using metrical data, then used the ellipses as models in the diagrams. I did not plot the specimens used for calculating the ellipses, but type specimens are plotted in bold letter abbreviations.

The materials used and the institutes in which are kept the materials seen are listed in the Appendix.

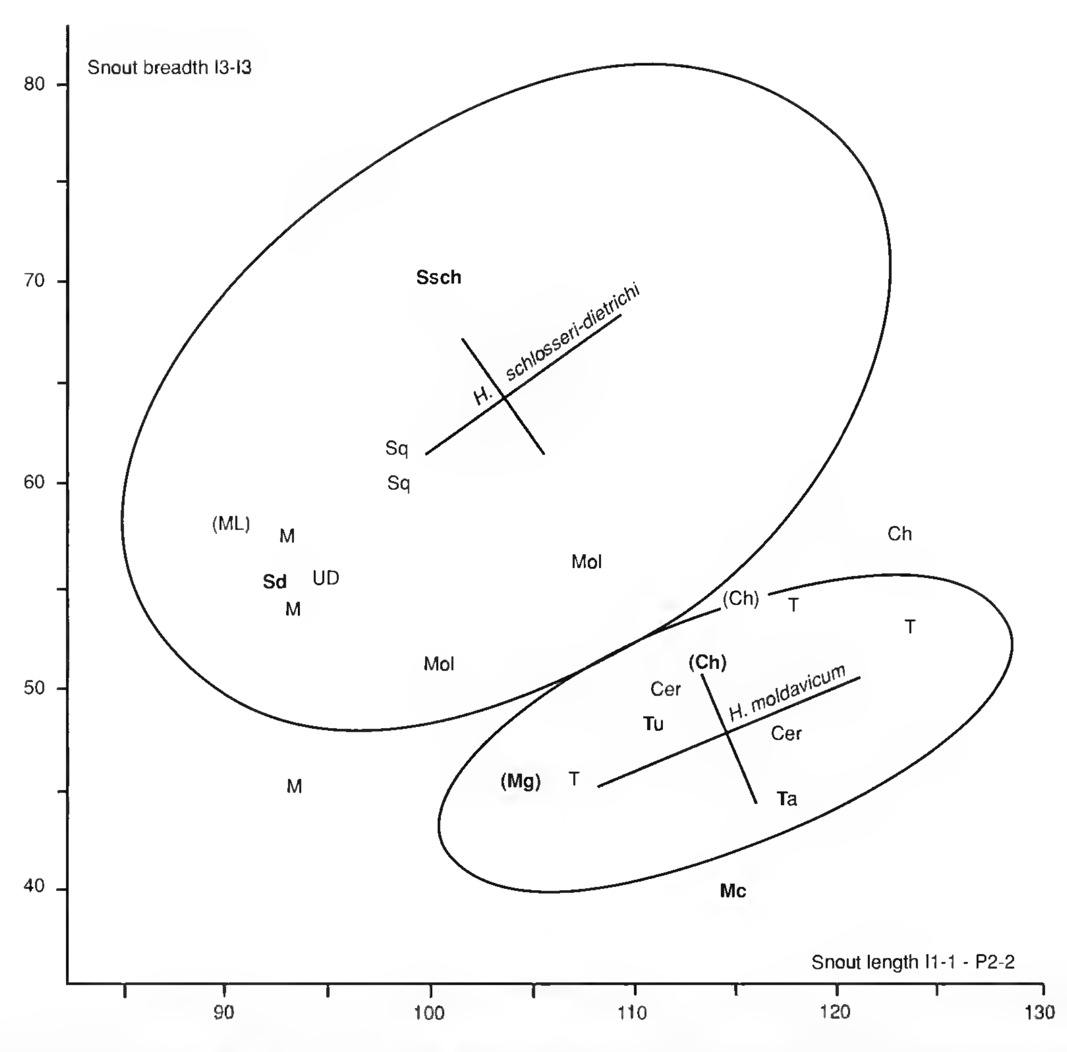


FIG. 1. — Upper snout breadth plotted to snout length in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens from the localities: **Cer**, Cherevichnoe; **Ch**, Chimislia; **K**, Karaslari; **M**, Maragheh; **ML**, Mt. Luberon; **Mol**, Molayan; **Sq**, Saloniki (coll. Arambourg & Puyhaubert); **T**, Tchobruchi; **Tu**, Tudorovo; **UD**, Umen Dol. Bold type abbreviations in figure depict type specimens: **Ch**, *H. pregiganteum* (Chisnau 4040/84); **Mc**, *H. campbelli* (Univ. California Riverside No. 13/1342); **Mg**, *H. gettyi* (Wien No. 840); **Sd**, *H. dietrichi* (Münster S I/7); **Ssch**, *H. schlosseri* (Wien 1911 V 114); **Ta**, *H. moldavicum* (Moscow PIN 1256-3639); **Tu**, *H. tudorovense* (OGUM 1780). Observations in parentheses approximative.

DESCRIPTION

EUROPE AND THE NEAR EAST

Hipparions with a short and/or broad snout

Hipparion prostylum Gervais, 1849 [localities: Mt. Luberon, France; Saloniki, Greece; Karaslari and Umen Dol, Macedonia (former Yugoslavia); possibly Maragheh, Iran], *H. schlosseri-dietrichi* Antonius, 1919-(Wehrli, 1941) [Samos without exact locality (Sondaar 1971, pl. II: a); Samos Q1, Q4, Q6 (Sondaar 1971, pl. II: b); Vathylakkos, Prochoma-1, Ravin des Zouaves (Koufos 1987, fig. 3), Greece; Basiboz (Forsten & Garevski 1989, photos 3, 4), Macedonia; and Maragheh] have a short and broad snout (Fig. 1: upper ellipse). The snout is short also in relation

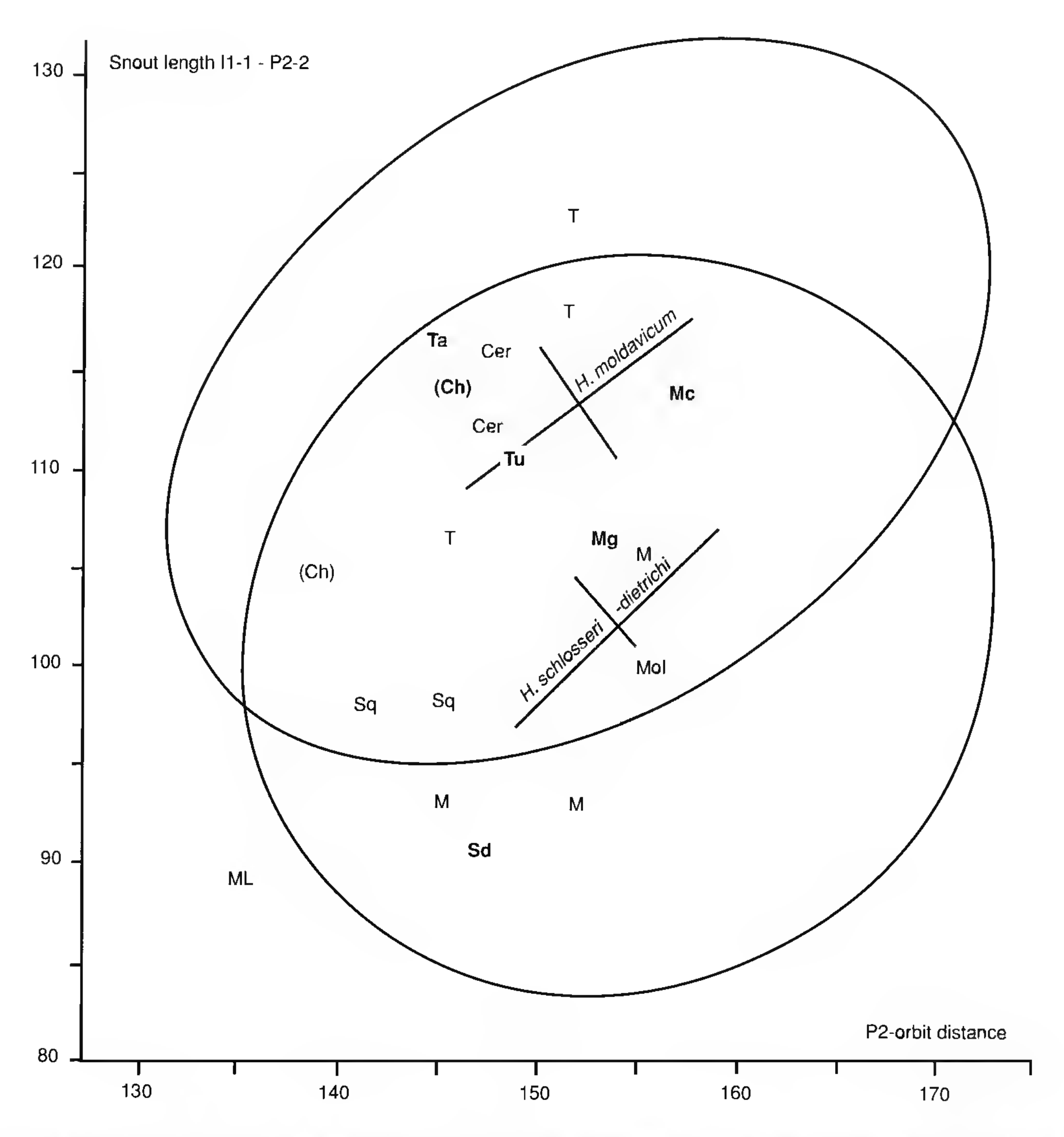


Fig. 2. — Upper snout length plotted to P2-orbit distance in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens from: **Cer**, Cerevichnoe; **Ch**, Chimislia; **M**, Maragheh; **ML**, Mt. Luberon; **Mol**, Molayan; **Sq**, Saloniki; **T**, Tchobruchi. Bold type abbreviations in figure depict type specimens: **Ch**, *H. pregiganteum*; **Mc**, *H. campbelli*; **Mg**, *H. gettyi*; **Sd**, *H. dietrichi*; **Ta**, *H. moldavicum*; **Tu**, *H. tudorovense*. Observations in parentheses are approximative.

to skull length (Fig. 2: lower ellipse) and in the lower jaw the snout is broad in relation to the length of the symphysis (Fig. 3: upper ellipse). The single preorbital fossa of the skull is placed rather far in front of the orbit. It may be faintly delimited and shallow or well-defined, in either case more or less pocketed. There is no clear difference in skull morphology between the smaller specimens (e.g. *H. prostylum* and the holotype of *H. dietrichi*, Münster SI/7) and the larger ones

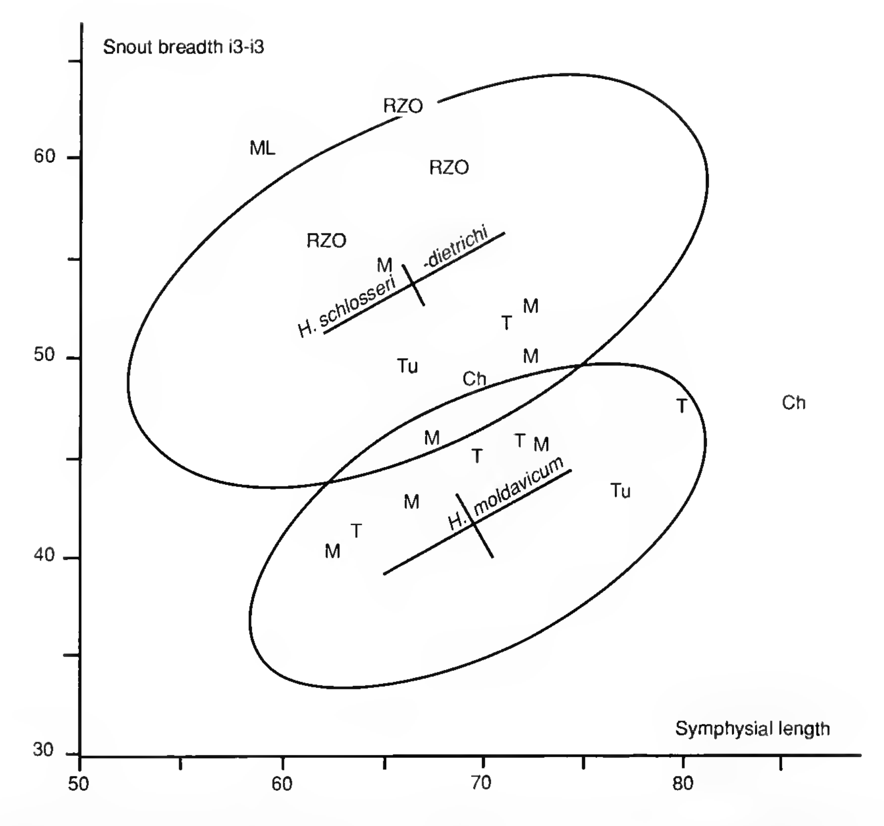


FIG. 3. — Lower snout breadth plotted to symphysial length in European hipparion jaws; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens from: **Ch**, Chimislia; **M**, Maragheh; **ML**, Mt. Luberon; **RZO**, Ravin des Zouaves; **T**, Tchobruchi; **Tu**, Tudorovo.

(e.g. Wien 1911 V 114, the holotype of *H. schlosseri*, and Budapest No. 274) (Figs 1, 2: ML, and in bold: Sd, Ssch). The names *schlosseri* and *dietrichi* were given the same species; although Antonius' name "*schlosseri*" is older, there is some uncertainty as to its validity (inadequate description and illustration of the type). Until the question as to the correct name is solved, I use both united by a hyphen: *H. schlosseri-dietrichi*.

In this group also belongs *H. molayanense* Zouhri, 1992 described from Molayan, Afghanistan (Zouhri 1992). In the two skulls seen, the snout is short, but not as broad as in the former group (Zouhri 1996, pl. 59) (Figs 1, 2: Mol). The preorbital fossa resembles that of the former group in being shallow, oval-egg-shaped, and situated far in front of the orbit.

The above mentioned short- and broad-snouted hipparions, *H. prostylum*, *H. schlosseri-dietrichi*, and *H. molayanense*, also have a short nasal opening, anteriorly either blunt or softly pointed, ending at a level well in front of P2. The nasal opening is short also compared with snout and skull length, except in Paris Mol. 040 from Molayan.

Among the skulls with a short-broad snout fall the type and the referred specimen of *H. garedzicum* Gabuniya, 1959 from Udabno, Georgia (Fig. 4: U, in bold). The nasal opening is short, ending at a level in front of P2 but the preorbital fossa is well-defined and deep (see Gabuniya 1959, pl. VI: 1). On the other hand, among skulls with a shallow preorbital fossa situated far from the orbit can be mentioned the specimen B-50 from Bazaleti, Georgia, referred to as

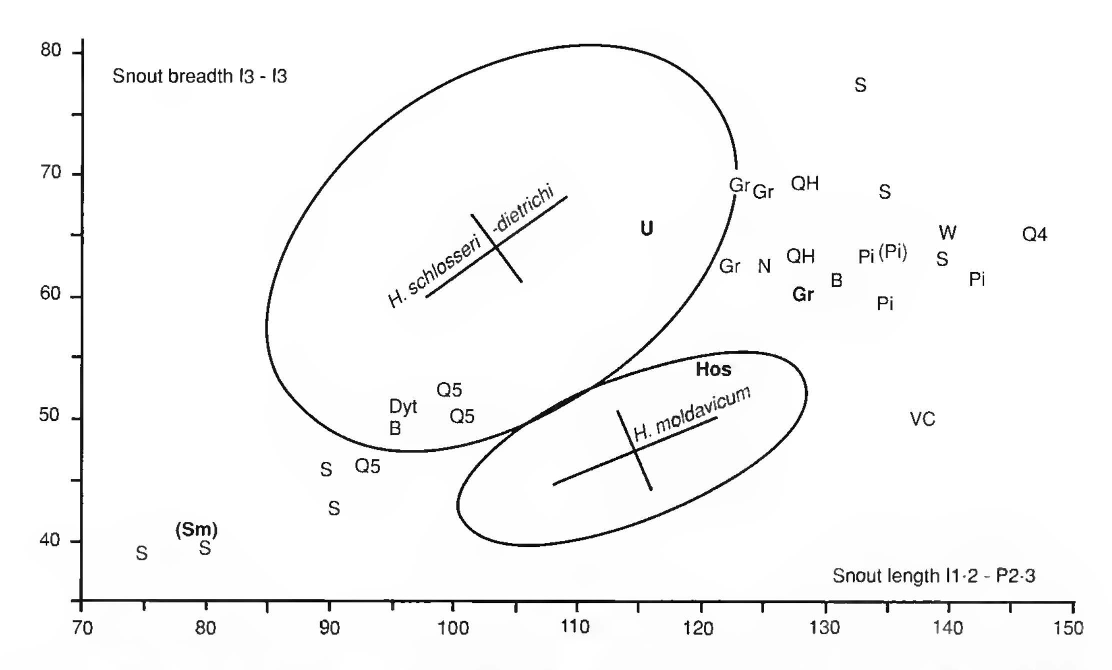


Fig. 4. — Upper snout breadth plotted to snout length in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of *H. matthewi* (scatter to the left) from: **B**, Beluska; **Dyt**, Dytiko (data Koufos 1988, table 1); **Q5**, Samos Q5; **S**, Samos without exact locality. Plotted also hipparions in the *H. primigenium* group (scatter to the right) from: **B**, Beluska; **VC**, Vila de Caballs; **Gr**, Grebeniki; **N**, Nesebr; **QH**, Oued el Hammam; **Pi**, Pikermi; **Q4**, Samos Q4; **S**, Samos without exact locality; **U**, Udabno; **W**, Inzersdorf. Bold type abbreviations in figure depict type specimens: **Gr**, *H. giganteum* (OGUM 1015); **Hos**, *H. catalaunicum* (BMNH 16397); **Sm**, *H. matthewi* (Budapest Ob/557); **U**, *H. garedzicum* (Tbilisi No. 156/13).

H. garedzicum by Meladze (1967, table VIII) and as *H. molayanense* by Zouhri (1992, 1996), but which differs from both in the snout being long and narrow (Fig. 5: Bz to the far right in diagram). The type skull of *H. tudorovense* Gabuniya, 1959 (OGUM 1780; Gabuniya 1959, pl. V: 2) from Tudorovo, Moldova, also has a shallow preorbital fossa situated relatively far in front of the orbit, but a narrow snout (Figs 1, 2: Tu, in bold). The nasal opening in B-50 from Bazaleti and OGUM 1780 from Tudorovo ends level with P2. A very fragmentary skull (Inst. of Paleobiology, Tbilisi No. 148/191; Gabuniya 1959, pl. VI: 3) from Kiourtevioul, 50 km north of Lake Urmia, Iran, the holotype of *H. urmiense* Gabuniya, 1959 has a shallow and faint fossa and a nasal opening extending level with P2-P3. Since the snout is lacking and the orbits are not visible, the placement of the preorbital fossa in relation to the orbit and the snout proportions are unknown.

A relatively broad snout is characteristic of the skull of *H. matthewi* Abel, 1926 [localities: Samos Q5 (Sondaar 1971, Pl. Ia-b) and Samos without exact locality data (*H. nicosi* Bernor & Tobien, 1989), Ravin de la Pluie, Vathylakkos, and Prochoma-1 (*H. macedonicum* Koufos, 1984; Koufos 1987, fig. 8), Dytiko (*H. matthewi* and *H. periafricanum* Villalta & Crusafont, 1957; Koufos 1987), Saloniki, Greece (coll. Arambourg & Puyhaubert); ?Umen Dol and Beluska, Macedonia; and Ploski Blagoevradsko (*H. microtatum* Nikolov, 1971), Bulgaria] but the relative breadth is less than in the *H. prostylum/schlosseri-dietrichi* group (Figs 4, 6: scatter to the left in diagram). In the lower jaw the snout is medium broad relative to symphysial length (Fig. 7: scatter to the left in diagram). The preorbital fossa in *matthewi* varies from well-defined to almost absent; in some specimens from Q5 it is double, consisting of a posterior fossa proper and an anterior, smaller subnasal fossa (Forsten

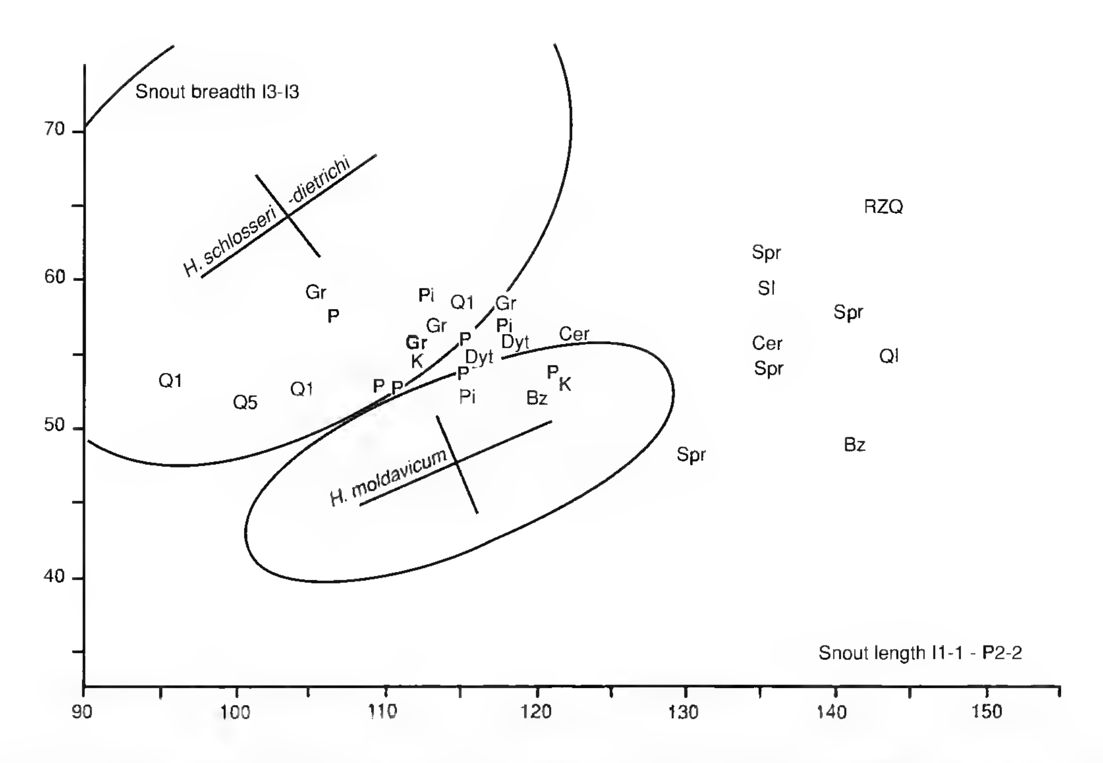


Fig. 5. — Upper snout breadth plotted to snout length in European hipparions; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality data) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of: *Hipparion verae* (**Gr**, Grebeniki; **K**, Karaslari); *H. mediterraneum* [**Bz**, Bazaleti (specimen B-51 to the left in diagram); **Dyt**, Dytiko (data Koufos 1988, table 1); **Pi**, Pikermi (data partly Koufos 1987, table 1)]; *Hipparion* sp. with a double fossa (**Q1** and **?Q5**, Samos quarries); *Hipparion* sp. (**P**, Piera). Plotted are also skulls of *H. proboscideum* (scatter to the right in diagram) from: **Cer**, Cherevichnoe; **RZO**, Ravin des Zouaves; **Spr**, **Sl** and **Q1**, Samos quarries. The skull B-50 from Bazaleti with a weak fossa falls in among the specimens of *H. proboscideum*. Bold type abbreviation in figure depicts type: **Gr**, *H. verae* (OGUM 1016).

1983). The nasal opening in *H. matthewi*, like snout length, varies from short to long or from a level 1 cm in front of P2 to level with P3 parastyle. The fragmentary nasal opening in München 1899 VII 31b (*H. nicosi* holotype) from Samos extends level with P2 and is thus comparable to the holotype of *matthewi* (Budapest OK/557), also from Samos. In the rather long-snouted specimens with a double fossa from Samos Q5, the nasal opening is long. The skulls of *H. matthewi* from Q5 resemble some larger skulls with a double fossa found from Samos Q1-Andriano (see Forsten 1983, fig. 3), possibly also from Samos Q5 and Gülpinar, Turkey (Figs 5, 8: Q1, Q5); they are here referred to as *H.* sp. (with a double fossa). They have a relatively short-broad snout and the nasal opening ends level with P2, but both the snout and the nasal opening are longer in relation to skull and snout length, respectively, than in *H. schlosseri-dietrichi* of similar size and from the same localities. This unnamed taxon seems to be related to the hipparions in the *H. mediterraneum* (Roth & Wagner, 1855) group, in which the fossa is situated close to the orbit, but is rarely double. The proportions of the snout and the depth of the nasal opening in these specimens from Samos are like in *H. mediterraneum* from Pikermi, Greece, but relatively broader and deeper, respectively, than in the various local forms of *H. moldavicum* Gromova, 1952 from Moldova and Ukraine, belonging in the same species group.

Hipparions with a long snout and/or nasal opening

Extreme for its long and narrow snout among

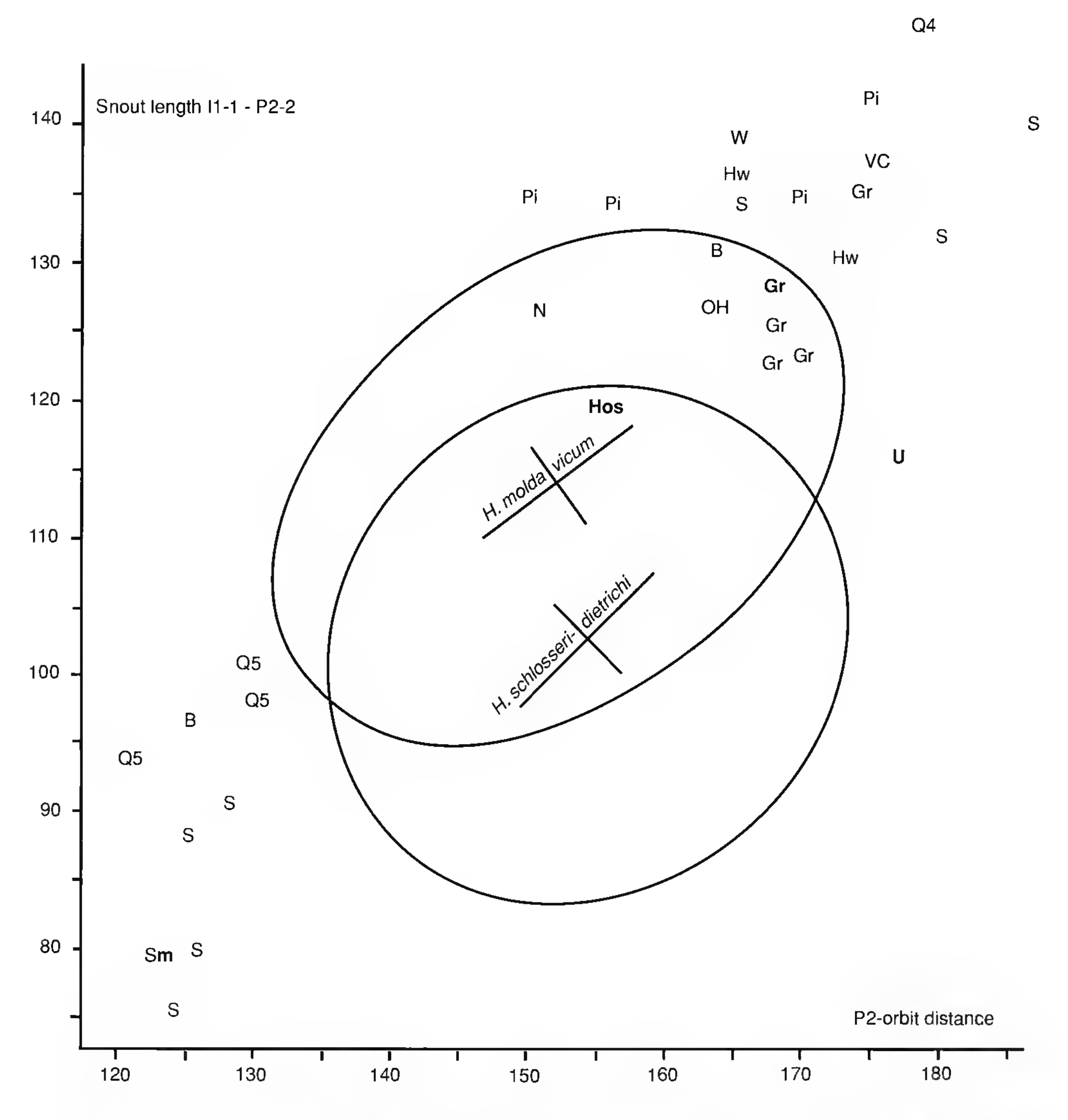


FIG. 6. — Upper snout length plotted to P2-orbit distance in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of *H. matthewi* (scatter to the left in diagram) from: **B**, Belushka, **Q5** and **S**, Samos quarries. Plotted are also specimens of the *H. primigenium* group (scatter to the right) from: **B**, Beluska; **Gr**, Grebeniki; **Hos**, Hostalets; **Hw**, Höwenegg; **N**, Nesebr; **OH**, Oued el Hammam; **Pi**, Pikermi; **Q4** and **S**, Samos quarries; **U**, Udabno; **VC**, Vila de Caballs; **W**, Inzersdorf. Bold type abbreviations in figure depict type specimens: **Gr**, *H. giganteum*; **Hos**, *H. catalaunicum*; **Sm**, *H. matthewi*; **U**, *H. garedzicum*.

the European hipparions is the specimen B-50 from Bazaleti with a shallow fossa (Meladze 1967, table VIII) (Figs 5, 8: Bz to the far right and top centre in diagram). Specimen B-51 from the same locality, but with a maximally developed, double preorbital fossa, has a medium long snout similar in its breadth: length proportions to that in *H. moldavicum* (Meladze 1967, table VII) (Figs 5, 8: Bz in centre of diagram). In both specimens the snout is longer than in *H. mediterraneum*, and in the lower jaw (Meladze 1967, table IX) the symphysis is longer and the

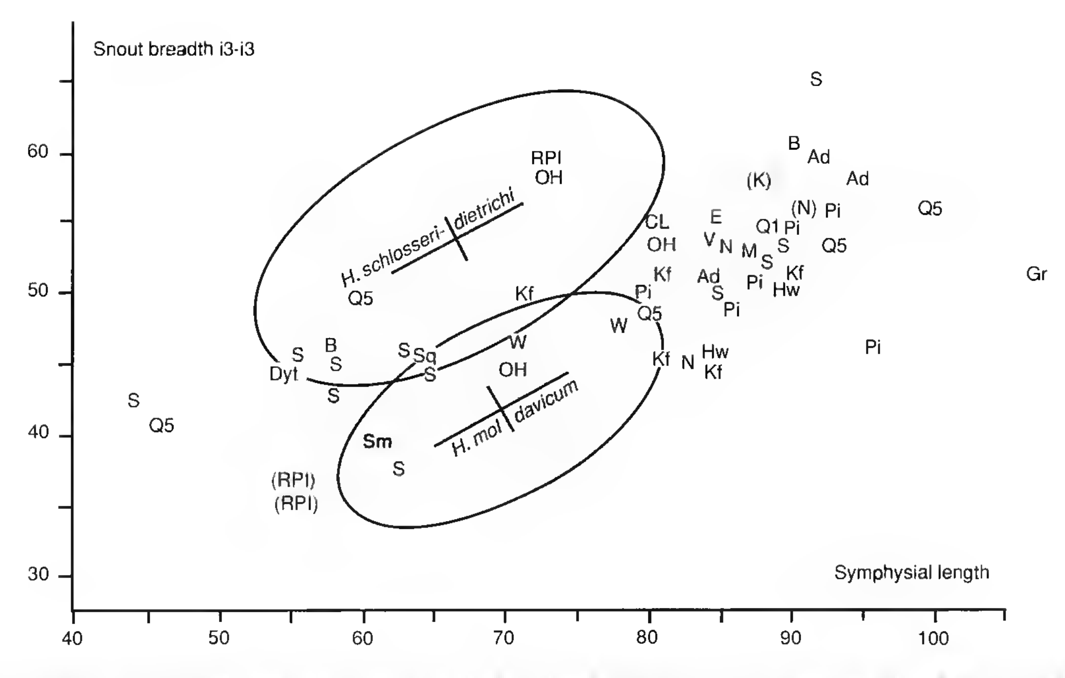


FIG. 7. — Lower snout breadth plotted to symphysial length in European hipparion jaws; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavotovka). Plotted are specimens of *H. matthewi* (scatter to the left) from: **B**, Beluska; **Dyt**, Dytiko (data Koufos 1988, table 2); **Q5** and **S**, Samos quarries; **RPl**, Ravin de la Pluie; **Sq**, Saloniki. Plotted are also (scatter to the right in diagram) not separable specimens of hipparions of the *H. primigenium* group and *H. proboscideum* from: **Ad**, **S**, **Q1** and **Q5**, Samos quarries; **B**, Beluska; **CL**, Can Llobateres; **E**, Eppelsheim; **Gr**, Grebeniki; **K**, Karaslari; **Kf**, Kalta; **M**, Maragheh; **N**, Nesebr; **OH**, Oued el Hammam; **Pi**, Pikermi; **RPl**, Ravin de la Pluie; **V**, Vozarzi; **W**, Inzersdorf and Wienerberg. Bold type abbreviations in figure depict type specimens: **Sm**, *H. matthewi*. Observations in parentheses are approximative.

snout narrower (Fig. 9: Bz). Compared for their nasal opening depth, that in B-50 is absolutely shorter than in B-51, but in both specimens the nasal opening reaches level with P2.

Hipparion sp. from Piera, Spain, has a well-defined, pocketed, pear-shaped to rounded triangular preorbital fossa and a long snout in relation to skull length (Forsten 1968, pl. 2) (Figs 5, 8: P). For its breadth, the snout resembles that in *H. mediterraneum* and *H. verae* Gabuniya, 1959 (Fig. 5: P, Pi, Gr). The nasal opening is short, ending from a level 2 cm in front of P2 to level with P2 paracone; it is short also in relation to snout and skull length.

Hipparion proboscideum Studer, 1911 [localities: Samos Q1 and Samos without exact locality data (Studer 1911, figs 1, 3, 4a; Sondaar 1971, pl. IIIa-d), Ravin des Zouaves (Koufos 1987, fig. 3), Greece; Vozarzi and Karaslari, Macedonia (Forsten & Garevski 1989, photos 1, 2); Valea Sarii, Romania (Forsten 1980); Kavakdere, Turkey; and Cherevichnoe, Ukraine, (*H.* sp. cf. *proboscideum* Forsten & Krakhmalnaya, 1997, fig. 7)], with an arrangement of the double preorbital fossa similar to that in specimen B-51, has a narrow snout similar to that in B-50, but the snout is not long in relation to skull length (Figs 5, 8: Spr, SI, QI, RZO, Cer). The nasal opening is long and deep, extending from level with P2 parastyle to P3 mesostyle. In its snout proportions *H. proboscideum* resembles the second large species from Samos Q1-Andriano and Q4, called *H.* cf. *proboscideum* and *H. primigenium* (v. Meyer, 1829) (Sondaar 1971, pl. III: e; Forsten 1983, in Appendix referred to as *H.* aff. *brachypus* Hensel), in which the single preorbital fossa and nasal opening are as deep as in the former, but in which the snout is longer in relation to skull length and broader than in *H. proboscideum* (Figs 4, 6: S, Q4). This taxon,

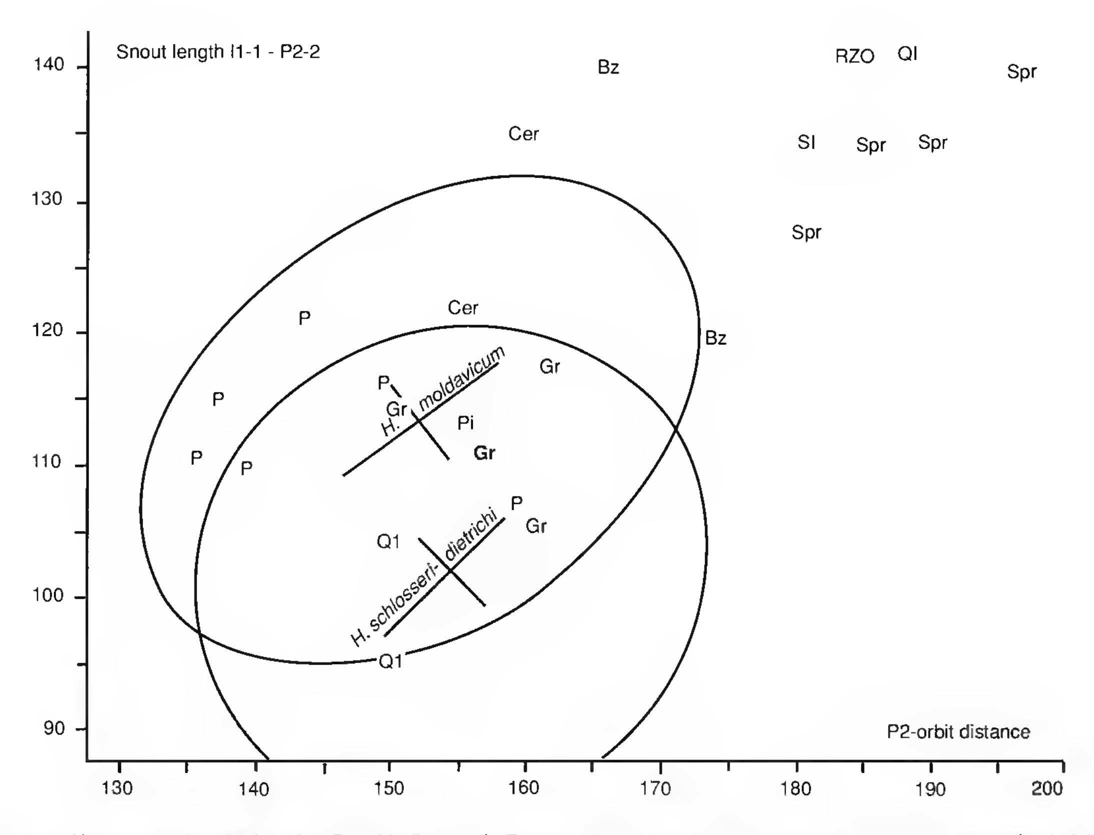


FIG. 8. — Upper snout length plotted to P2-orbit distance in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of *H. mediterraneum* [**Bz**, Bazaleti (specimen B-51 in centre of diagram); **Pi**, Pikermi]; *H. verae* (**Gr**, Grebeniki); *Hipparion* sp. with a double fossa (**Q1**, Samos O1); and *Hipparion* sp. (**P**, Piera). Plotted are also specimens of *H. proboscideum* (scatter to the right) from: **Bz**, Bazaleti (specimen B-50 in top-centre of diagram); **Cer**, Cherevichnoe; **Q1**, **Sl** and **Spr**, Samos quarries; **RZO**, Ravin de Zouaves. Bold type abbreviation in figure depicts type: **Gr**, *H. verae*.

similar to the large one from Pikermi (*H. brachypus* Hensel, 1862, see Koufos 1987: pl. III) (Figs 4, 6: Pi), leads over to hipparions with a mostly long snout, comprising the *H. mediterraneum* and the *H. primigenium* species groups.

Hipparions with a medium long and narrow snout

A medium long and narrow snout characterizes the local samples of *H. moldavicum* [localities: Tarakliya, Novoelizavetovka, Tudorovo, Chimishlia, Cherevichnoe, and Chiobruchi, Ukraine and Moldova, possibly Maragheh, Iran) (Gromova 1952, tables I-III; Gabuniya 1959, pls III: 2, 3, IV: 1, 2; Watabe & Nakaya 1991; Forsten & Krakhmalnaya 1997, fig. 6) (Figs 1, 2: lower and upper ellipse, respectively)]. The nasal opening extends from a level 1 cm in front of P2 to P2 mesostyle; it is short in relation to snout and skull length. In the lower jaw the snout is narrow in relation to symphysial length (Fig. 3: lower ellipse). *Hipparion moldavicum* has a well-defined, single preorbital fossa placed close to the orbit, a character which it shares with *H. mediterraneum* from Pikermi, but has a narrower snout and shorter nasal opening even taking into account its smaller skull size. Similar narrow snout proportions are found in skulls from Maragheh, described as *H. gettyi* Bernor, 1985 and *H. campbelli* Bernor, 1985 (Bernor 1985), in OGUM 1780 (type of *H. tudorovense*) from Tudorovo, and in the type skull (Kishinev 4040/84) of *H. praegiganteum* Tarabukin, 1967 from Chimishlia, Moldova (Figs 1, 2: Tu, Mg, Mc, Ch, in bold). The single preorbital fossa of

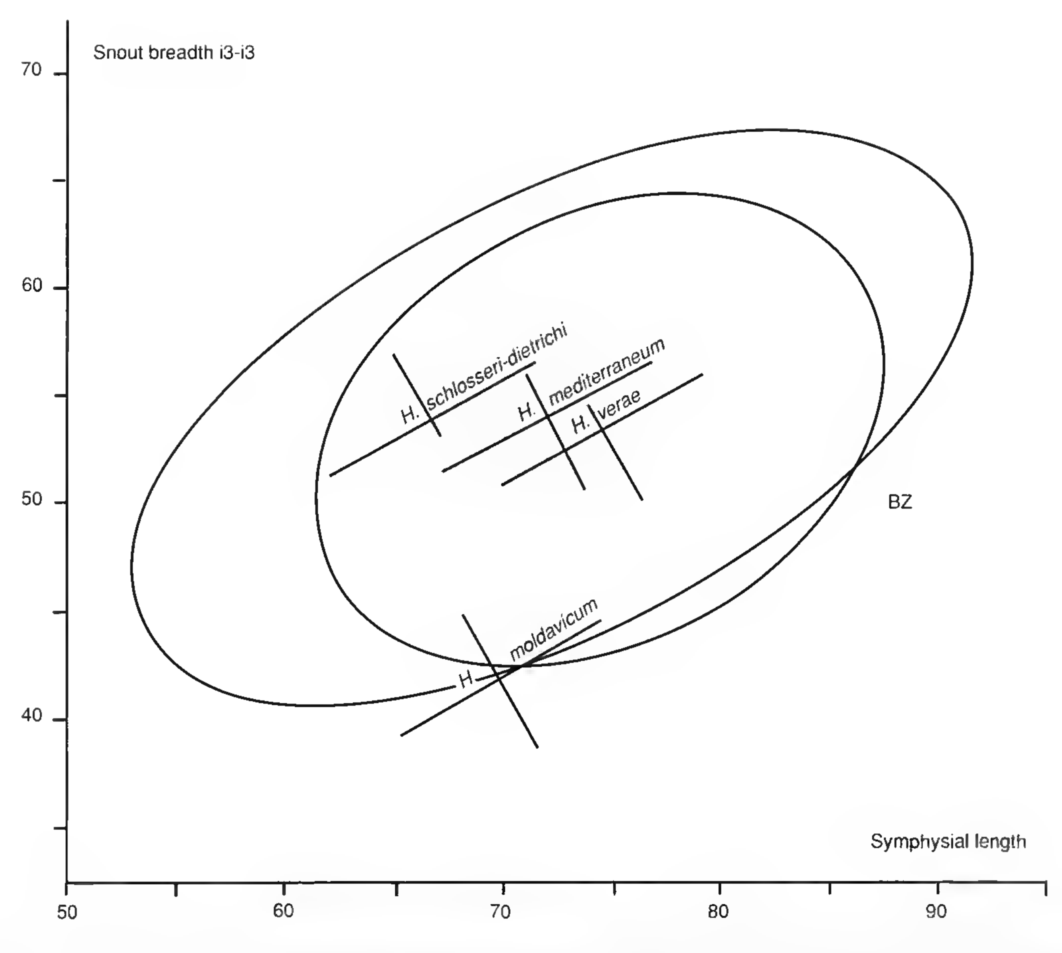


FIG. 9. — Lower snout breadth plotted to symphysial length in European hipparion jaws; measurements in mm; 95% equiprobability ellipses calculated and drawn for *Hipparion mediterraneum* from Pikermi and *H. verae* from Grebeniki. Axes also drawn on the data of *H. schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted is single specimen B-54 jaw from **Bz**, Bazaleti.

these skulls is rounded triangular to oval, shallow or with a posterior pocket, and situated moderately far from the orbit. The nasal opening ends level with P2; it is particularly long in relation to snout and skull length in the type skulls (Wien, No. 8401 and BMNH 44574/cast of Univ. California Riverside No. 13/1342) of *H. gettyi* and *H. campbelli* from Maragheh. *Hipparion gettyi* may be a younger synonym of *H. tudorovense*, with which it shares similar snout proportions and proportions between the orbit-fossa: P2-orbit distances, and similar extension of the nasal opening. *Hipparion campbelli* may be a younger synonym of *H. urmiense*, with which it shares a similar long tooth row and the extension of the nasal opening (see Watabe & Nakaya 1991).

Hipparions with a medium long and broad snout

Although similar in the shape and placement of the preorbital fossa, *H. mediterraneum* (Pikermi and Dytiko, Greece, Koufos 1987, pls I, II; Koufos 1988, pls 1, 2; possibly Maragheh, Iran, and Bazaleti, Georgia) has a broader snout than *H. moldavicum*, although overlapping the latter in snout proportions (Figs 5, 8: Pi, Dyt). The nasal opening is deeper, reaching level with P2, even with P2-P3.

Hipparion verae from Grebeniki, Moldova, has

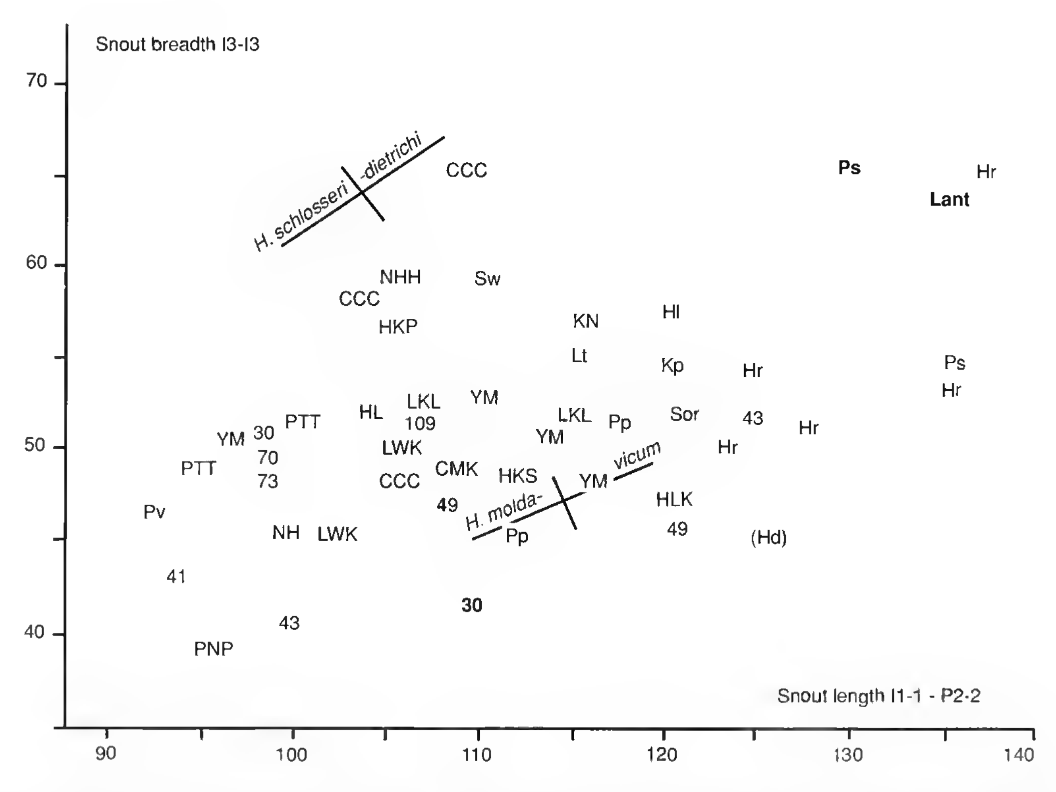


FIG. 10. — Upper snout breadth plotted to snout length in Asiatic hipparions; measurements in mm. For comparison the axes are drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Abbreviations: **CCC**, Chang Chia Chuang and 2 miles W of Chang Chia Chuang; **CMK**, Ch'eng Chia Mao Kou; **Hd**, *Hipparion dermatorhinum*; **HKP**, Hsiao Ku Po; **HKS**, Hsiao Kou Shan; **Hl**, *H. licenti*; **HL**, Hsi Liang; **HLK**, Huang Lu Kou; **Hr**, *Proboscidipparion rocinantis* (various locations); **KN**, Khirgis Nur; **Kp**, Kalmakpai; **Lant**, Lantian; **LKL**, Lu Kao Ling; **LT**, Ling Tou; **LWK**, Liao Wang Kou; **NH**, Nan Ho; **NHH**, Nan Hao Hsia; **PNP**, Po Niu Po; **Pp**, *P. "pater"*; **Ps**, *P. sinense*; **PTT**, Pai Tao Tsun; **Sor**, Sor; **Sw**, Siwaliks; **YM**, Young Mu Kou; **30**, Loc. 30; **43**, Loc. 43; **44**, Loc. 44; **49**, Loc. 49; **70**, Loc. 70; **73**, Loc. 73; **109**, Loc. 109. Bold type abbreviations in figure depict the types: **49**, *H. plocodus* Sefve, 1927 (Uppsala No. 3824), **30**, *H. fossatum* Sefve, 1927 (Uppsala No. 3821), **Lant**, *H. weihoense* Liu, Li & Zhai, 1978 (IVPP V 3113.1); **Ps**, *Proboscidipparion sinense* Sefve (Uppsala No. 3925 & 3926).

snout proportions resembling those of *H. mediterraneum* (Gabuniya 1959, pls II: 1, 3, III: 1, VIII: 2) (Figs 5, 8: Gr, Pi). In the lower jaw of both forms the snout is broad in relation to the length of the symphysis (Fig. 9: Gr, Pi), even resembling the jaws of the *H. prostylum/schlosseri-dietrichi* complex. *Hipparion verae* has a differently shaped and placed preorbital fossa and the nasal opening is shallower than in *H. mediterraneum*, reaching from a level 2-1 cm in front of P2 to P2 mesostyle. Like in the latter, the preorbital fossa is occasionally double.

In skulls from Basiboz, Umen Dol and Karaslari (Macedonia, former Yugoslavia), referred to as *H. verae* in Forsten & Garevski (1989, photos 5-7), the preorbital fossa spills into the fossa buccinator, in some cases forming an isolated, anterior subnasal fossa level with P2. In these specimens the placement, shape and depth of the preorbital fossa varies, as does the depth of the nasal opening (ending from 1 cm in front of P2 to level with P2 paracone). The snout is medium broad in two measureable specimens (PMM Kar 86/73 and Kar 203/73), belonging either to this species or to *H. prostylum/schlosseri-dietrichi* (Fig. 5: K).

Hipparions lacking a preorbital fossa

The earliest known *Hipparion* in Europe lacking

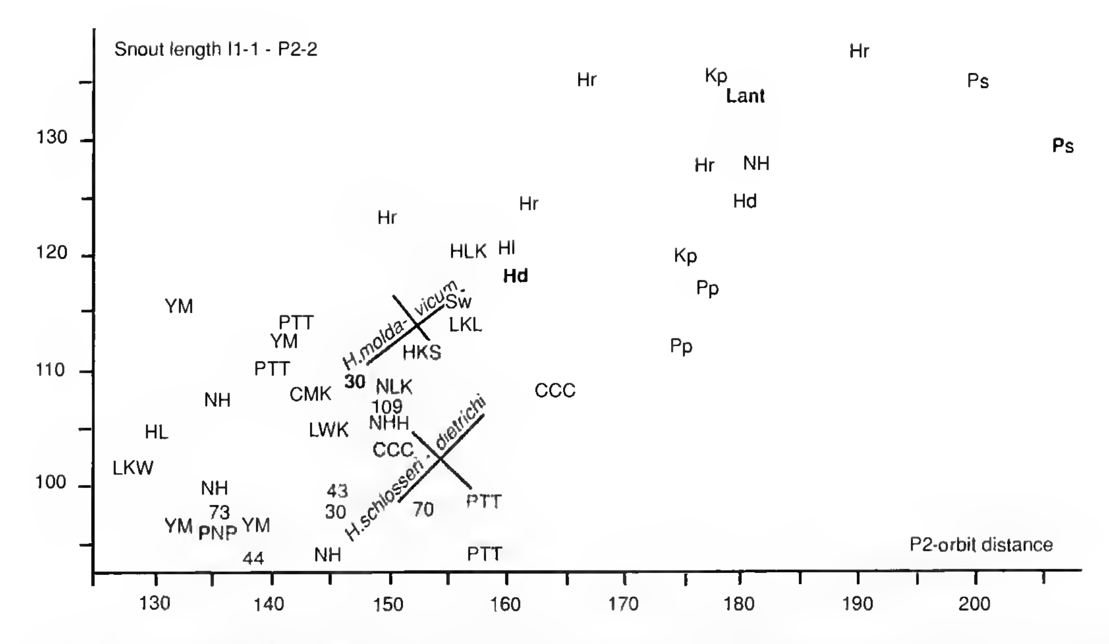


FIG. 11. — Upper snout length plotted to P2-orbit distance in Asiatic hipparions; measurements in mm. For comparison are drawn the axes calculated on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). For abbreviations see Figure 10. Bold type abbreviations in figure depict types: **Hd**, *H. dermatorhinum* (Uppsala No. 3872); **Lant**, *Hipparion weihoensis*; **Ps**, *Proboscidipparion sinense*; **30**, *H. fossatum*.

a preorbital fossa is *H. platygenys* Gromova, 1952 from the Meotian of Tarakliya (Gromova 1952, table IV). Its upper snout is unknown, but in three lower snouts the symphysis is long and the snout medium broad in the measureable specimens. Gromova (1952) referred the specimen PIN 1256-3634 to *H.* sp. or *H. platygenys*. *Hipparion platygenys* may be a junior synonym of *H. hippidiodus* Sefve, 1927 from China (see below).

From the Pliocene is known *Proboscidipparion rocinantis* (Hernandez-Pacheco) from Villaroya, Spain, and Kvabebi, Georgia, lacking or with a faintly defined preorbital fossa. This species represents the dentally advanced caballoid hipparions, referable to a genus of their own: *Proboscidipparion* Sefve, 1927 (Forsten 1997). The snout of the skull and jaws from Villaroya is long and medium broad; that of the skull from Kvabebi (Vekua 1972, Ris. 27-28, tables XVIII, XIX) is short and broad. The nasal opening is short, ending in front of or level with P2, respectively. *Proboscidipparion rocinantis* is also found in China and Mongolia, where specimens tend to have a narrow snout (see below).

The Hipparion primigenium *group*

Among the early (Vallesian) forms of this group represented by skulls with snouts are the hipparions from Vila de Caballs and Hostalets, Spain (*H. catalaunicum* Pirlot, 1956; Pirlot 1956, pl. V); Höwenegg, Germany; Inzersdorf, Austria; Nesebr, Bulgaria (*H. presulcatum* Nikolov, 1971 and *H. nesebricum* Bakalov & Nikolov, 1962; Nikolov 1971, table I: 1, 1a); Kalfa and Braila, Moldova (*H. sarmaticum* Lungu, 1973; Lungu 1973, Ris. 1, table I); and Oued el Hammam, Algeria (*H. africanum* Arambourg, 1959); later (Turolian) forms are found at Udabno, Georgia (*H. garedzicum* Gabuniya, 1959, pl. VI: 1); Samos Q1-Andriano and Q4 (*H.* cf. *proboscideum* Sondaar 1971, pl. IIIe; here *H.* aff. *brachypus*), Pikermi (*H. brachypus* Koufos, 1987, pl. III), and Grebeniki (*H. giganteum* Gromova, 1952, table XII), evidently also at Beluska, Karaslari, and Vozarzi, Macedonia. While the early forms have a triangular or oval fossa, in the later forms the fossa is pear-shaped. The snout is long and broad (Figs 4, 6), but the length of the nasal opening varies considerably between the local samples. It is very shallow in the specimens

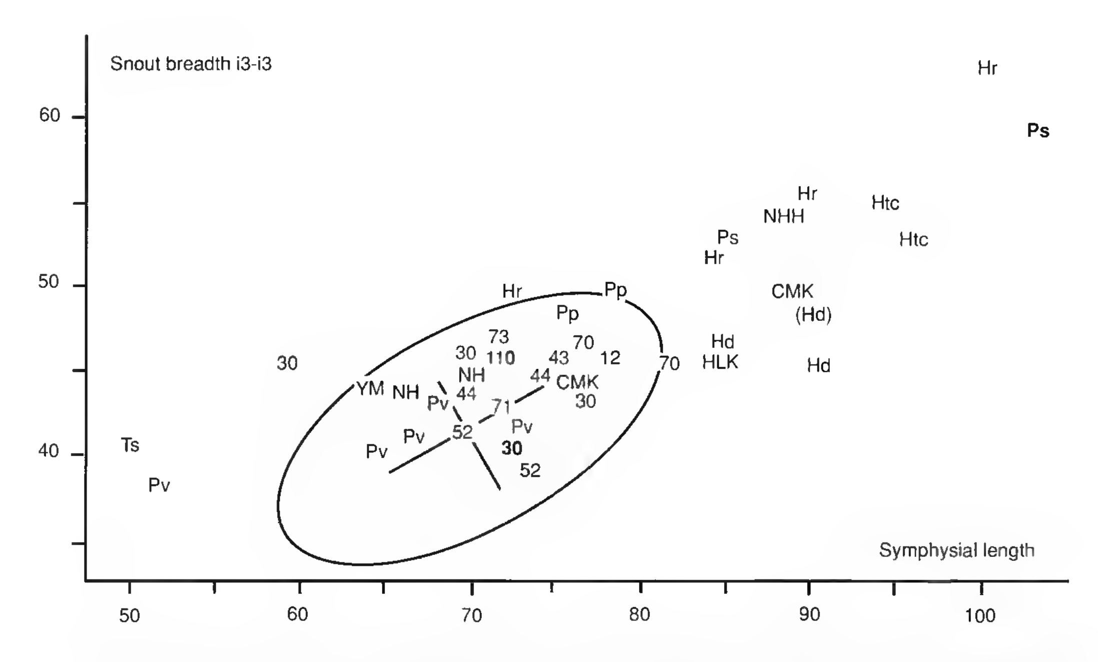


FIG. 12. — Lower snout breadth plotted to symphysial length in Asiatic hipparion jaws; measurements in mm. Abbreviations as in Figure 10, in addition to **Htc**, *Hipparion tchicoicum*; **Ts**, Tan Tsun; **12**, Loc. 12; **52**, Loc. 52; **71**, Loc. 71; **110**, Loc. 110. Bold type abbreviations in figure depict types: **Ps**, *Proboscidipparion sinense*; **30**, *Hipparion fossatum*.

from Hostalets (ending 3 cm in front of P2), Inzersdorf (3-2 cm), Kalfa (2-1 cm), Höwenegg (3-1 cm), Udabno and Grebeniki (from 1-2 cm in front of P2 to P2 anterior tip); medium deep from Vila de Caballs (level with P2 anterior tip), Oued el Hammam (just in front of P2 to P2 paracone), and Nesebr (P2 mesostyle); and deep in the skulls from Pikermi (P2 mesostyle-P3 paracone) and Samos Q1-Andriano (level with P3). *Hipparion garedzicum* from Udabno (see above) differs from the rest of the group in having a short snout relative to skull length (Figs 4, 6: U, in bold).

In the lower jaw the snout is broad in two (MNHN 89, 143), narrow in a third (MNHN 98) of the jaws from Oued el Hammam; it is also broad in the jaw (Univ. Thessaloniki, RPl-1) from Ravin de la Pluie, Greece, referred to as *H. primigenium* (Koufos 1986), and from Can Llobateres (Fig. 7: OH, RPl, CL). In the other local samples in this group the lower snout tends to be narrow and the symphysis long, particularly in the large forms from Pikermi, Samos, and Grebeniki.

ASIA

Hipparions with a short and broad snout

There are few hipparions in Asia with as pronouncedly short and broad a snout as the members of the *H. prostylum/schlosseri-dietrichi* group. Most Asiatic hipparions, e.g. all the Chinese species kept in Uppsala described by Sefve (1927) and the majority of the specimens in the AMNH, have a narrow snout (Figs 10, 12). As for snout length in relation to the distance P2-orbit, there are both long and short-snouted forms (Fig. 11). The conformation of the nasal opening and the nasals show great variation among the finds, as does the preorbital fossa.

A skull (New York, AMNH 19761) from 0.5 mile south-west of Dhok Pathan, Pakistan, called *H. antelopinum* Falconer & Cautley, 1847 (Matthew 1929), has a medium long but broad snout (Figs 10, 11: Sw) and a small, although posteriorly deep, preorbital fossa placed far in front of the orbit. The nasal opening ends at a level 1 cm in front of P2 and is short also in relation to snout and skull length. The species represented by this skull seems to be a vicar of the

European-Near Eastern *H. prostylum/schlosseri-dietrichi* group mentioned above.

From Chang Chia Chuang, Shanxi, China, there are two skulls (AMNH 44-B 421 juv. and 44-B 427) in which the snout is quite broad (Fig. 10: CCC). The preorbital fossa, situated far from the orbit, is small and oval-pearshaped; the nasal opening appears short. From 2 miles west of Chang Chia Chuang, there are two skulls (AMNH 21-B 38 and 25-B 49), the one with a broad, the other with a narrow snout (Fig. 10: CCC); the snout is also short in relation to skull length (Fig. 11: CCC). The nasal opening is anteriorly pointed and deep, extending level with P2 metacone-P3 mesostyle. The deep fossa is situated close to the orbit. Of these skulls, AMNH 21-B 38 with a nasal opening extending level with P3 mesostyle, resembles the peculiar Chinese *H. licenti* Qiu, Huang & Guo, 1987 (Qiu *et al.* 1987, pls IX, XII) (Beijing, IVPP THP 20764, 20767, 20769 juv. and London, BMNH 44577/cast of F:AM 125708), characterized by its strongly retracted nasal opening, reaching level with M1 mesostyle, but evidently unreduced nasals. The snout in *H. licenti* is known only in BMNH 44577 and is rather long and medium broad (Figs 10, 11: HI). The preorbital fossa is double, the posterior one situated close to the orbit (Qiu *et al.* 1987, fig. 26).

A skull from Nan Hao Hsia (AMNH 35-B 255) has a medium long and broad upper snout, but the snout of the jaw of the same specimen is narrow (Figs 10-12: NHH). The nasal opening is very short, ending 2 cm in front of P2; the preorbital fossa is pear-shaped. A skull from Hsiao Ku Po (AMNH 53-B 641) resembles the previous one in having a broad snout (Fig. 10: HKP), very short nasal opening, and a pear-shaped preorbital fossa.

Hipparion elegans Gromova, 1952 from Pavlodar, Kazakhstan, resembles some *H. matthewi* in having a relatively broad upper snout (Fig. 10: Pv), as well as in the placement and shape of the single preorbital fossa (Gromova 1952, table V; Forsten 1983, fig. 4). The nasal opening seems short, extending from 1 cm in front, to the anterior tip, of P2. The five measureable lower jaws correspond to those of some *H. matthewi* in the snout being narrow (Fig. 12: Pv). This species is an Asiatic vicar of the dwarf *H. matthewi*, from which it differs in the morphology of its teeth and in the proportions of its limb bones.

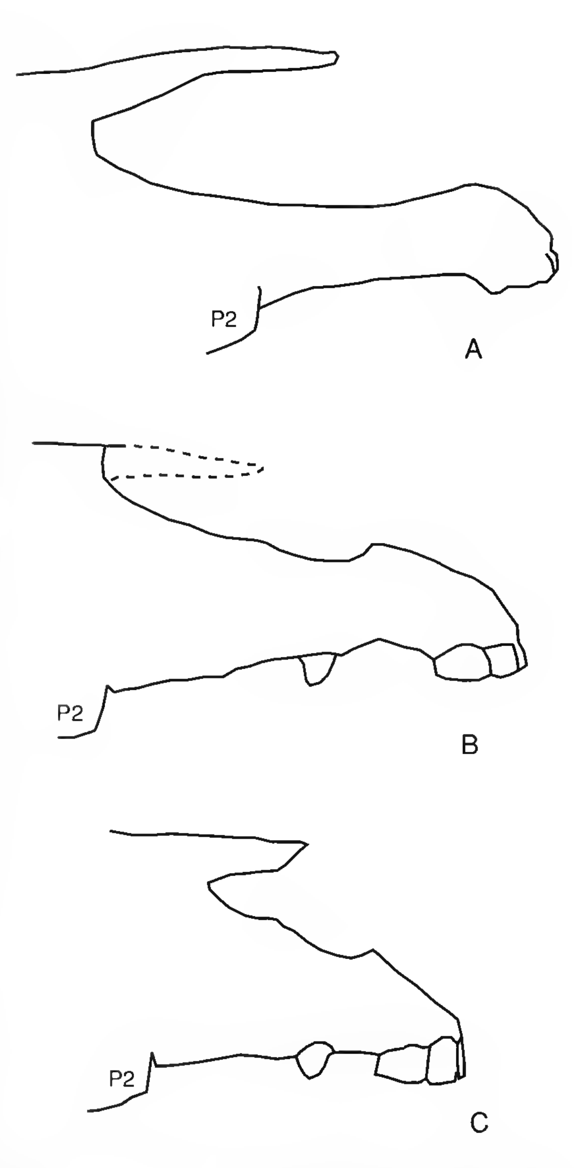


Fig. 13. — **A**, upper snout of *H. dermatorhinum*, showing deep nasal opening and long, low snout; holotype, Uppsala No. 3872, subadult (after Sefve 1927, table I: 1); **B**, upper snout of *H. moldavicum*, showing medium deep nasal opening and snout; holotype, PIN 1256/3639 (after Gromova 1952, table I: 3); **C**, upper snout of *H. giganteum*, showing very short nasal opening; holotype, OGU 1015 (after Gromova 1952, table 12: 2). Drawings not to scale.

Hipparions with a narrow snout

Extreme among the Asiatic hipparions with a

long and narrow snout is *H. tchicoicum* Ivaniev, 1966 (Qiu *et al.* 1987, pl. XIII); the snout is narrow also in the lower jaw and the symphysis long (Fig. 12: Htc). The nasal opening is very short, ending at a level almost 2 cm in front of P2; it is short also in relation to snout length. The large preorbital fossa is evidently situated close to the orbit (orbit not visible).

Hipparion dermatorhinum Sefve, 1927 from China has a long snout in relation to skull length, and the snout is low and narrow (Sefve 1927, table I: 1-3; Qiu *et al.* 1987, pls XLI, XLII) (Figs 10, 11: Hd). In the lower jaw the snout is similarly narrow and the symphysis long (Fig. 12: Hd). The nasal opening is retracted, reaching level with P3, it is long also in relation to snout and skull length; the nasals are unreduced. The preorbital fossa is well-defined but shallow.

An upper snout from Sor, Tadzhikistan, shows the presence of a double preorbital fossa (Zhegallo 1978, Ris. 73). The narrow snout (Fig. 10: Sor), the nasal opening extension, and the double fossa closely resemble those in the specimen B-51 from Bazaleti.

Hipparions lacking a preorbital fossa

A skull (PIN 2433-360) from Kalmakpai, Kazakhstan, referred to as *H. hippidiodus* because it lacks a preorbital fossa (Zhegallo 1978, Ris. 61), has a long, narrow snout but may be laterally crushed, since a second specimen (PIN 2433-460) from the same locality has a medium broad snout (Figs 10, 11: Kp). In both specimens the nasal opening ends level with the metacone of P2. Originally *H. hippidiodus* was described from Loc. 115, Kingyang, China (Sefve 1927; Forsten 1968, pl. 3; Qiu *et al.* 1987, pl. XXXVIII); its snout is unknown.

Skulls from Khirgis Nur-2, Mongolia, called *H. mogoicum* Zhegallo (Zhegallo 1978), also lack a fossa. The snout in the measureable specimen is medium broad like in PIN 2433-460 from Kalmakpai, but shorter (Fig. 10: KN). The nasal opening reaches level with P2 mesostyle.

Chinese hipparions belonging in the species or species group *Proboscidipparion rocinantis-houfenense* (Hernandez-Pacheco)-(Teilhard & Young, 1931) with advanced, caballoid cheek teeth and lacking a preorbital fossa (see above), have a long snout in relation to skull length and the snout is narrow (Qiu *et al.* 1987, pls VI, VII; Forsten 1997, fig. 7) (Figs 10, 11: Hr); also the snout of the lower jaw is narrow (Fig. 12: Hr). The nasal opening is short, extending from 0.5 cm in front of P2, to level with P2 paracone.

There are four skulls of the two (?) species of typical *Proboscidipparion*, *P. sinense* Sefve (Sefve 1927, table VI: 22-24, VII) and "*pater*" Matsumoto, 1927 (Qiu *et al.* 1987, pls I-IV). The snout is rather short in relation to skull length and narrow (Figs 10, 11: Pp, Ps and Ps in bold). Also the symphysis is short, taking into account the size of the jaw, and the snout is narrow (Fig. 12: Ps and Ps in bold). The nasal opening is enormously retracted, extending from level with M1 metacone to M2 mesostyle, and the nasals are reduced and foreshortened. There is no fossa.

DISCUSSION

Phylogenetic and functional considerations

There are differences between local forms (species, subspecies, local populations) of hipparions for the proportions of the snout and the extension of the nasal opening, but within a local form these characters are quite stable. Characters of the snout and nasal opening occur in combination with different shapes and placement, even absence, of the preorbital fossa. Snout breadth: length proportions are not correlated with the extension of the nasal opening. How to delimit species and supraspecific groups when characters of the snout, nasal opening and nasals, and preorbital fossa are distributed mosaic-like, as are characters of the teeth and limb-bone size and proportions? What do these characters and the differences between forms signify? Do they have phylogenetic and functional significance? Which characters should be given more, which less weight when phylogenies are discussed and reconstructed? How to determine which characters are primitive, which derived, *i.e.* morphocline polarities?

The hipparions (*Hipparion*, *Proboscidipparion*

Sefve, 1927, *Neohipparion* Gidley, 1903, *Nannippus* Matthew, 1926, and *Pseudhipparion* Ameghino, 1904) can be distinguished from the ancestral merychippines on the basis of the cheek teeth in the lower jaw, particularly the lower molars. The lower molars of the merychippines retain a primitive, low double knot with little differentiated and rounded metaconid and metastylid loops, while in the hipparions the loops of the molar double knot are well differentiated, thus advanced. All Eurasian and African hipparions are true hipparions, with well-differentiated loops of the double knot of the lower molars, indicating dispersal to the Old World at a stage when the dental pattern already had become modernized.

In the hipparions, a short snout and short nasal opening could be considered primitive, since they characterize the merychippine ancestors, e.g. "*Neohipparion coloradense*" (originally of Osborn, 1918) from the early Barstovian of Boulder Quarry, Nebraska, and late Barstovian of NE Colorado (MacFadden 1984, figs 52, 54, 58, 59), and "*Cormohipparion*" *goorisi* MacFadden & Skinner, 1981 from the late Barstovian of Trinity River Pit 1, Texas (MacFadden 1984, figs 121, 123). On the other hand, if a short-broad snout in a hipparion is an adaptation to grazing, it should be considered a late, advanced character, since grazing evolved with the spread of c4 grasses about 7-5 Ma ago (Cerling *et al.* 1993). Some merychippines, although dentally primitive, already had a rather long snout, *e.g.* "*Eoequus*" *wilsoni* Quinn, 1955 (Quinn 1955, pls 10: 1-3, 11: 1-3, 12, 13), which although larger is probably closely related to "*Hipparion*" *shirleyi* MacFadden, 1984 (both are from Texas and Barstovian in age; MacFadden 1984, figs 28, 29). On the other hand, some North American hipparions or near-hipparions, although dentally advanced, retained a short snout and nasal opening, e.g. "*Neohipparion affine*" (originally of Leidy, 1869) from the late Clarendonian of Upper Miller Quarry, Nebraska (MacFadden 1984, fig. 63), "*Cormohipparion*" *sphenodus* (originally of Cope, 1885) from the Valentinian of Railway/Railroad Quarry, Nebraska (MacFadden 1984, figs 124, 126), and "*Cormohipparion*" *occidentale* (originally of Leidy, 1856) from the late Clarendonian of Gidley Horse Quarry, Texas (MacFadden 1984, figs 133, 136). The breadth of the snout in relation to snout length is not given in these horses.

The nasal opening in the North American hipparions does not extend posteriorly beyond the level of P2, but often ends at a level 1-4 cm in front of P2 (MacFadden 1984, table 1). Although in the Eurasian hipparions the nasal opening may be equally short, e.g. in early *H. primigenium*, the snout is generally longer in relation to skull length. In the *H. prostylum/schlosseri-dietrichi* group both the nasal opening and snout are short. In the Eurasian hipparions a deep nasal opening, posteriorly extending to a level beyond P2, has evolved several times and in combination with differently shaped, even absent, preorbital fossae, e.g. in the large *Hipparion* from Samos Q1-Andriano and Pikermi, in *H. proboscideum*, *H. licenti*, *H. dermatorhinum*, and *Proboscidipparion sinense*. The deep nasal opening in some hipparions has given rise to hypotheses that these horses had a tapir-like proboscis (Sefve 1927; Solounias & Dawson-Saunders 1988). In extant mammals with a lengthened nose, e.g. tapirs, elephants, saiga and dik diks, the nasal bones are foreshortened, thus allowing mobility of the nose (Macdonald 1984). In most of the known hipparions with an exceptionally deep nasal opening, the nasals are normally long. Only in some *Proboscidipparion* (*sinense* and "*pater*") are the nasals reduced in length, the nasal opening between the premaxillas is narrowly slit-like, and the upper symphysis long. Sole among the hipparions the snout in these *Proboscidipparion* does resemble that in a tapir (Sefve 1927). However, the deep nasal opening and foreshortened nasal bones in these *Proboscidipparion* also resemble those in a moose, *Alces alces* (Linnaeus, 1758), which has no proboscis but a large overhanging upper lip. Extant horses, which have a moderately deep nasal opening and long nasals, have very mobile lips. The hipparions may, to a varying degree, also have had mobile lips useful for gathering grass or browse.

In the extant horses the diverticulae nasi form blind sacks in connection with the nostrils and occupy the nasal opening (Ellenberger & Baum

1943; but see Gregory 1920). The longer and wider the nasal opening, the more room for the diverticulae. According to Gregory (1920) the diverticulae in extant *Equus* (Linnaeus, 1758) partly occupy the shallow subnasal (= preorbital) fossa. In the hipparions nasal opening extension and development of the fossa are not correlated. Well-developed and posteriorly deep in the large hipparions from Samos Q1-Adriano and Pikermi, the fossa is small and situated far from the nostrils in *H. licenti*, and is absent in *Proboscidipparion sinense* and "*pater*". The diverticulae comprise the vomeronasal organ with sensory pathways to the hypothalamus. The vomeronasal organ is believed to be involved with the "flehmen", *i.e* olfactorial tasting of feromones (Estes 1972), and with certain low vocalizations.

The generally narrow snout in Old World hipparions may have to do with these horses having been chiefly browsers or mixed-feeders (Hayek *et al.* 1991). Candidates for the grazing niche would be the broad-snouted forms in the *H. prostylum/schlosseri-dietrichi* complex and *H. antelopinum*. Eisenmann (1998) recently plotted least diastemal breadth to symphysial length in jaws of Old World hipparions. She differentiated specimens with a broad and those with a narrow jaw (Eisenmann 1998, figs 3, 4) and discussed jaw proportions and incisor morphology in relation to mode of feeding (whether grazing or browsing). With a few exceptions her diagrams correspond to mine, plotting lower snout width to symphysial length. The exceptions are specimens probably wrongly identified, e.g. in her figure 3 No. 7, 8 are evidently *H. verae* not *giganteum*, and No. 9 is not *H. mediterraneum*.

Taxonomic considerations

In hipparion taxonomy and phylogeny, the preorbital fossa is often given more weight than other characters, sometimes even at the near exclusion of other characters (see Eisenmann *et al.* 1987). Solely on the alleged resemblance of the fossa, the narrow-snouted *H. gettyi* (= *H. tudorovense*?) and *H. campbelli* (= *H. urmiense*?) with a long nasal opening are said to be the ancestor and descendant, respectively, of the short and broad-snouted *H. prostylum* with a short nasal opening (Bernor *et al.* 1996). The members in the *H. prostylum/schlosseri-dietrichi* group are believed to have given rise to hipparions lacking a preorbital fossa, although there are no signs that the fossa did disappear in this group. *Hipparion hippidiodus/platygenys* from Tarakliya, the earliest known hipparion lacking a fossa, has a medium broad snout and is of the same age as the members in the former group, while the hipparions from Khirgis Nur-2 and Kalmakpai, also lacking a fossa, may be younger. Their nasal opening is deep and long. On the supposed similarity of the fossa the long-snouted, large hipparion from Samos Q1-Andriano, with a deep and long nasal opening, is referred to as *H. giganteum* (Bernor *et al.* 1996), the type form of which has a very short nasal opening. On the other hand, *H. macedonicum* is believed to represent a species different from *H. matthewi* (Koufos 1986; Bernor *et al.* 1996), although identical to that species in skull and jaw morphology, metapodial size and proportions, and in protoconal length and plication count of its teeth. Some of these conflicting identifications seem to have been dictated by the presumed stratigraphic position of the find, rather than by its morphology. However, stratigraphic position is not a taxonomic character.

Hipparion multiple dispersal?

Old World Hipparion has been thought to represent multiple dispersals from North America. This idea was also based on preorbital fossa morphology, ignoring the morphology of the cheek teeth and snout, and the faunal evidence against multiple equid dispersal. In the Miocene the North American equid fauna was diverse, comprising anchitheriines, para-merychippines, pliohippines, and hipparions, often several genera of each group in the same faunas (Forsten 1989). Of the anchitheriines only *Anchitherium* v. Meyer, 1834 dispersed to the Old World, none of the para-merychippines or pliohippines made it, and there is no evidence that more than one hipparion successfully crossed the Bering intercontinental connection. None of the typical North American hipparionid (sub)genera *Pseudhipparion*, *Neohipparion*, or *Nannippus* has

ever been found in the Old World. Neither has any of the several Eurasian hipparions with a deep nasal opening ever been found in North America.

CONCLUSIONS

It is dangerous to base hipparion taxonomy, systematics and phylogeny, and hypotheses about intercontinental dispersal, on single characters, *e.g.* on the preorbital fossa alone (Eisenmann *et al.* 1987). Skulls are rare, most fossil samples consist of isolated teeth and limb bones, which in multispecies samples may be difficult/impossible to objectively couple with the skulls or identify to species. The more characters that are taken into account, the more difficult is the delimitation of species and lineages, because of the mosaic combination of characters (see also Eisenmann 1998). I believe that genera of equids should be characterized on their cheek teeth, particularly on the cheek teeth of the lower jaw. Within a genus occur subgroups (species groups, in some cases worthy of subgeneric separation), which sometimes can be circumscribed on several characters in common, *e.g.* plication count of the upper cheek teeth, proportions of the limbs, preorbital fossa morphology, and snout proportions. Many finds cannot be placed within a single subgroup, as they share characters with several. There is no reason why the preorbital fossa should have priority in determining subgroup membership, but neither has any other character. Reference to species or species group should be based, if possible, on the holomorph of the find.

Stratigraphic provenance is not a taxonomic character. Stratigraphic schemes, using species of fossil horses as markers, should be regarded with suspicion. More often than not they are idealized and do not truly reflect the time range of the fossil species, which often occur at an earlier date and/or survive for a longer time than presupposed by the schemes. Subjective "morphological trends", often consciously or unconsciously constructed to fit and/or to support alleged stratigraphic successions, are equally suspicious.

Fossil equids should not be forced to fit a stratigraphy, but should be objectively interpreted against the background of stratigraphy.

Acknowledgements

My sincere thanks are due the curators and caretakers of the fossil collections studied for this paper (see Appendix). I also thank Dr. V. Eisenmann and an anonymous reviewer for useful comments on the manuscript.

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Submitted for publication on 2 April 1998; accepted on 31 July 1998.

APPENDIX

List of hipparion specimens used in this paper. Listed are only specimens, which have yielded measurements on the upper and/or lower snout. Listed are not specimens lacking or with fragmentary snout, although representing the same species, from the same localities, and present in the same collections. When studied in the 1960-ties, most collections were still inadequately filed, as reflected by the frequent lack of collection numbers.

Hipparion sp.
(with double preorbital fossa), not named.

LOCALITY. — Samos Q1 (and Q5?) and Samos without exact locality data.

AGE. — Turolian.

MATERIALS. — Samos: (AMNH 20628, probably 20599, 22908, 94905 & no No., all Q1) five skulls, (AMNH 94906 & no No., Q1) skull and jaw, possibly also (AMNH 20786 & 22912, Q5); (SMF no No. and possibly no No.) two jaws; Geological Museum, Lausanne (No. 151, 610, 843, Andriano) three jaws; Carnegie Museum, Pittsburgh (No. 2126) a jaw.
H. matthewi or *H.* sp (with a double fossa): Samos (AMNH 22928, Q5) jaw; (SMF no No.) two jaws; (MNHN 1955-1 73) a jaw.
H. sp. (with double fossa) or *H. schlosseri-dietrichi*: Samos (AMNH 20651, 20721 & no No., Q1; No. 10733) four jaws; Geol. Mus., Lausanne (Nos. 78 & 1031, Andriano) two jaws; Nat. Hist. Mus., Vienna (1911 V 135) a jaw.

Hipparion sp.
not named, not *H. mediterraneum*.

LOCALITY. — Piera, Spain.

AGE. — Turolian.

MATERIALS. — Institut Paleontologic Dr. M. Crusafont, Sabadell (IPS.P 6359, 6360, 6365, 6372, and two specimens without a readable number) skulls.

Hipparion africanum Arambourg, 1959

TYPE LOCALITY. — Oued el Hammam, Algeria.

AGE. — Vallesian.

MATERIALS. — (MNHN 141 & no visible No.) two skulls, (MNHN 89, 98, 143) three jaws.

Hipparion antelopinum Falconer & Cautley, 1847

TYPE LOCALITY. — Potwar Plateau, Siwaliks, Pakistan.

AGE. — Turolian.

MATERIAL. — (AMNH 19761) a skull.

Hipparion brachypus Hensel, 1862

TYPE LOCALITY. — Pikermi, Greece.

AGE. — Turolian.

MATERIALS. — Pikermi: British Museum of Natural History, London (BMNH unreadable No.) skull, (BMNH 11211, 11213 & 11217) three jaws; (MNHN no No.) skull, (MNHN 31 & three specimens without a number) four jaws; Geological Institute, Göttingen (no No.) skull; Swedish Museum of Natural History, Stockholm (no No.) jaw; Humboldt Museum, Berlin (no No.) skull; Yale Peabody Museum of Natural History (No. 11768) skull with jaw.
In addition: Natural History Museum, Basel (PK 89) a jaw of either *H. brachypus* or *H. mediterraneum*.
H. aff. *brachypus*: Samos: (AMNH 22838, Q4) a skull, possibly (AMNH 22912 & 22922, Q5); (SMF 4707) a skull, (SMF no No.) a jaw; Geol. Inst., Budapest (OK 425) a jaw; Nat. Hist. Mus., Vienna (No. 1911 V 118) a skull; Geol. Inst., Lausanne (No. 73 & 148, Andriano) skull & jaw, (No. 175, Andriano) a jaw; Hessisches Landesmuseum, Darmstadt (Ss 45) a jaw. — Beluska, Macedonia (former Yugoslavia): Prirodnjacki Muzej, Beograd (PM 2791) jaw. — Karaslari, Macedonia: (PMM 193/73) jaw. — Maragheh, Iran: (MNHN 561) a jaw.
H. aff. *brachypus* or *H. proboscideum*: Samos: (AMNH 20640, Q1) a jaw; Inst. of Geol. & Paleontol., Münster (Sl/no No.) a jaw.

Hipparion catalaunicum Pirlot, 1956

TYPE LOCALITY. — Hostalets de Pierola, Spain.

AGE. — Vallesian.

MATERIALS. — (BMNH 16397, type *H. catalaunicum*) a skull.

Hipparion dermatorhinum Sefve, 1927

TYPE LOCALITY. — Loc. 30, Bao De, Shanxi, China.

AGE. — Turolian.

MATERIALS. — Loc. 30: Paleontol. Inst., Uppsala (M 3872, type) skull. — Huang Lu Kou, China (AMNH 41-L 310) skull and jaw. — Bao De, Shanxi, China: (IVPP no No.) skull and jaw, (IVPP 8243?) skull and jaw, (IVPP no No.) jaw.

Hipparion elegans Gromova, 1952

TYPE LOCALITY. — Pavlodar, Kazakhstan.

AGE. — Turolian.

MATERIALS. — (PIN no visible No.) a skull, (PIN 2346-2479, -2516, -4883, 2413-2847, -2864) five jaws.

Hipparion garedzicum Gabuniya, 1959

TYPE LOCALITY. — Udabno, Georgia.

AGE. — Late Vallesian-Early Turolian.

MATERIALS. — Musei Grusii, Tbilisi (156/13 type *H. garedzicum* & 270/34) two skulls.

Hipparion giganteum Gromova, 1952

TYPE LOCALITY. — Grebeniki, Moldova.

AGE. — Early Meotian/Late Vallesian/Early Turolian.

MATERIALS. — (OGU 1012/2, 1015 type & 1017) three skulls, (OGU 1018) skull and jaw, (OGU unreadable No.) a jaw.
In addition OGU 908, a skull, is intermediate between *H. verae* and *H. giganteum*.

Hipparion hippidiodus Sefve, 1927

TYPE LOCALITY. — Loc. 115, King Yang Hsien, Gansu, China.

AGE. — ?Turolian.

MATERIALS. — Kalmakpai, Kazakhstan: (PIN 2433-340, -360, -340) three skulls.

Hipparion licenti Qiu, Huang & Guo, 1987

TYPE LOCALITY. — Sianhotsun, Tchangkou, Yushe, Shanxi, China.

AGE. — Ruscinian.

MATERIAL. — (BMNH 44577, cast F:AM 125708) skull.

Hipparion matthewi Abel, 1926

TYPE LOCALITY. — Samos without exact locality data.

AGE. — Late Vallesian to and including Turolian.

MATERIALS. — Samos, Greece: (AMNH 22907 & 22936, Q5) two skulls, (AMNH no No., Q5) a jaw; (SMF 4710 & no No.) two skulls, (SMF no No.) a jaw; Nat. Hist. Mus., Vienna (no No.) a skull; British Museum of Natural History, London (BMNH 14071, cast of type) skull & jaw; Geol. Inst., Budapest (OK 557, type of *H. matthewi*) skull and jaw. — Ravin de Pluie, Greece: University of Thessaloniki (RPI-21 type *H. macedonicum* Koufos & RPI-36) two jaws. — Beluska, Macedonia (former Yugoslavia): Prirodnjacki Muzej, Beograde (PM 2659/197 & 2751) two jaws.

Hipparion mediterraneum (Roth & Wagner, 1855)

TYPE LOCALITY. — Pikermi, Greece.

AGE. — Turolian.

MATERIALS. — Pikermi (BMNH 11215) jaw; (MNHN no No.) skull and jaw, (MNHN 514-31 & no No.) two jaws; Nat. Hist. Mus., Vienna (no No.) a skull, (no No.) a subadult jaw; University of California Museum, Berkeley (UCM 63422) a jaw; US National Museum, Washington, D.C. (No. 267) a jaw; Swedish Museum of Natural History, Stockholm (no No.) two jaws; Geological Institute of the University, Göttingen (no No.) a jaw; Natural History Museum, Stuttgart (no No.) jaw to skull.
H. cf. *mediterraneum*: Bazaleti, Georgia: Institute of Paleobiology, Tbilisi (B-51) skull, (B-54) a jaw. — Maragheh, Iran: (MNHN no No.) a jaw; Nat. Hist. Museum, Vienna (no No., Ketchawa) jaw; National Museum, Praha (no No.) jaw.

Hipparion mogoicum Zhegallo, 1978

TYPE LOCALITY. — Khirgis Nur, Mongolia.

AGE. — Turolian.

MATERIALS. — Khirgis Nur: (PIN 3222-193 type & no No.) two skulls.

Hipparion molayanense Zouhri, 1992

TYPE LOCALITY. — Molayan, Afghanistan.

AGE. — Turolian.

MATERIALS. — (MNHN Mo 040 & 1758) two skulls.

Hipparion moldavicum Gromova, 1952

TYPE LOCALITY. — Tarakliya, Moldova.

AGE. — Meotian/Turolian.

MATERIALS. — Tarakliya: Paleontological Institute & Museum, Moscow (PIN 1256-2922, -3639 type, -3647, -3648 & no No.) five skulls, (PIN 1256-3619, -3620, -3638, -3641, -3642, -3643, -3700, -4189, -4191, -6605, -6944, -7027 & four without a number) jaws. — Novoelizavetovka, Ukraine: (OGU 1233, 1306, 1307, 1313, 1314, 1459, 3369, 3371) skulls, (OGU 1394-95, 1401, 1403, 1404) jaws. — Cherevichnoe, Ukraine: Dept. Paleontol. & Paleontol. Mus., Kiev: (No. 45-2665, -3849, -3925) three skulls. — Tchobruchi, Moldova: (OGU 3081) skull, (OGU 3078) two jaws; Mus. Ordzonikidze, Moscow (No. 2080 & no No.) two jaws, (No. 2026 & 2081) a skull and jaw may be either from Tchobruchi or Grebeniki.
H. aff. *moldavicum*: Novaya Emetovka-2, Ukraine:

Dept. Paleontol. & Paleontol. Mus., Kiev (No. 25-2439, -2923, -3005, -3200, -3310) skulls. — Chimishlia, Moldova: Institute of Geology & Paleontology, Univ. Bucharest (No. 66/(378), 378a & no No.) three skulls, (no No.) jaw; Regional Museum, Chisnau (No. 44040/79 & -/81) jaws. — Maragheh, Iran: (BMNH 3924) skull; (MNHN three specimens without No.) three jaws; Nat. Hist. Mus. Vienna (no No., Kopran & Ketchawa) two jaws.

Hipparion platygenys Gromova, 1952
(?younger synonym of *H. hippidiodus* Sefve 1927).

TYPE LOCALITY. — Tarakliya, Moldova.

AGE. — Meotian/Turolian.

MATERIALS. — (PIN 1256-2942, -3634 & no No.) three jaws.

Hipparion praegiganteum Tarabukin, 1967

TYPE LOCALITY. — Chimishlia, Moldova.

AGE. — Meotian/Turolian.

MATERIALS. — Regional Museum, Chisnau (No. 4040/84, type) skull, (No. 4040/83) jaw.

Hipparion primigenium (v. Meyer, 1829)

TYPE LOCALITY. — Eppelsheim, Germany.

AGE. — Vallesian.

MATERIALS. — Eppelsheim: Geol. Inst., Budapest (OK 22) a jaw. — Höwenegg, Germany: Humboldt Museum, Berlin (no No., cast) skull and jaw; Hessisches Landesmuseum, Darmstadt (Hö 58/VI) skull and jaw, (Hö. 54B) a jaw. — Vila de Caballs, Spain: (IPS no No.) skull and jaw. — Can Llobateres, Spain: (IPS no No.) jaw. — Inzersdorf, Austria: Natural History Museum, Vienna (SK 1346 & no No.) two skulls, (No. 1875 VI 5) a jaw. — Wienerberg, Austria: Nat. Hist. Museum, Vienna (1842 LVII 11) a jaw. — Prottes, Austria: Geological Institute, Univ. of Vienna (No. 958) a jaw. — Baltavar, Hungary: Geol. Inst., Budapest (No. 90) a jaw; Natural History Museum, Budapest (No. 319b, 390, 391) three jaws. — Nesebr, Bulgaria: Geological Institute, Univ. Sofia (No. 130) skull, (No. 40, 133 & no No.) three jaws.

Hipparion proboscideum Studer, 1911

TYPE LOCALITY. — Samos without exact locality data.

AGE. — Turolian.

MATERIALS. — Samos: (AMNH 20771, Q1, AMNH 20772, Q1s) two skulls; (SMF 4706, 4708, 4709) three skulls; (SI/4) a skull, (possibly SI/208) a jaw; (possibly BMNH 4359) a jaw. — Ravin des Zouaves: Univ. Thessaloniki (RZO-60) skull.

H. sp. (cf. *proboscideum*): Cherevichnoe, Ukraine: Dept. Paleontol. & Paleontological Museum, Kiev (No. 45-2664, -4282) two skulls.
H. proboscideum or *H.* sp. (with double fossa), Samos: (SI/277) a jaw.

Hipparion prostylum Gervais, 1849

TYPE LOCALITY. — Mt. Lébéron, France.

AGE. — Turolian.

MATERIALS. — Faculté des Sciences, Lyon (no No.) a skull with jaw; Faculté des Sciences, Montpellier (no No.) a lower snout.

Hipparion prostylum/H. schlosseri-dietrichi
an entity not well defined, resembling both species.

TYPE LOCALITY. — None, but present in southern Macedonia (former Yugoslavia) and northern Greece, possibly also in Maragheh, Iran.

AGE. — Turolian.

MATERIALS. — Saloniki, Greece: (Coll. Arambourg & Puyhaubert) Muséum National d'Histoire Naturelle, Paris (MNHN 1919-8) two skulls, (MNHN 1911-23) a jaw. — Ravin des Zouaves, Greece: University of Thessaloniki (RZO-76, -105, -145, -154) four jaws. — Karaslari, Macedonia (former Yugoslavia): Prirodonaucen Muzej na Makedonija, Skopje (PMM 86/73, 93/73 subadult & 203/73) skulls, (PMM 410/73) a jaw.
In addition: Umen Dol, Macedonia, (PMM 99/60) a skull of either *H. matthewi* or *H. prostylum/H. schlosseri-dietrichi*. — Maragheh, Iran: (MNHN three specimens without No.) three skulls.

Hipparion sarmaticum Lungu, 1973

TYPE LOCALITY. — Kalfa, Moldova.

AGE. — Middle Sarmatian/Vallesian.

MATERIALS. — Kalfa: Tiraspol Pedinstitut, formerly Tiraspol, now Chisnau (no No.) five jaws. — Braila, Moldova: (PIN 646-12) a skull.

Hipparion schlosseri-dietrichi
Antonius, 1919-(Wehrli, 1941)
Both names were given evidently the same species; Antonius' name is older, but possibly not valid (description incomplete, type not figured). Wehrli used the genus name *Hemihipparion*.

TYPE LOCALITY. — Samos without exact locality data.

AGE. — Turolian.

MATERIALS. — Samos, Greece: American Museum of Natural History, New York (AMNH 20596, 20598, 20608, 20692, 20997 & two without number, all Samos Q1) seven skulls, (AMNH 20603, 20650,

20655, 20667, 22787, all Q1) five jaws, (AMNH 22860, Q4 & no No., ?Q4) two skulls, (AMNH 22990, Q6) skull; Senckenberg Museum, Frankfurt (SMF no No.) three jaws; Natural History Museum, Vienna (No. 1911 V 114, type *H. schlosseri*); possibly Geological Institute, Budapest (No. 274) skull; Institute of Geology & Paleontology, Münster (SI/7, type *Hemihipparion dietrichi* & SI/28) two skulls, possibly (SI/236) a jaw; Teylers Museum, Haarlem (No. 15470 & no No.) two skulls; Geological Museum, Lausanne (No. 132) skull, (No. 84 & 195 from Samos, Andriano) two jaws; University of Texas-Austin, Bur. Econ. Geol. (No. 40275 cast of CMNH P. 12868) skull. — Maragheh, Iran: Nat. Hist. Mus. Vienna (no No., Kopran) jaw.

Hipparion tchicoicum Ivanjev, 1966

TYPE LOCALITY. — Beregovaya, Russia.

AGE. — Villafranchian.

MATERIALS. — Shamar, Mongolia: (PIN 3381-53) jaw. — Peihaitsun, Matsegou, Yushe, China: (IVPP THP 19009 & 19013) skull and jaw. —Yidjouantsun, Yushe, China (IVPP THP 10302) jaw.

Hipparion tudorovense Gabuniya, 1959

TYPE LOCALITY. — Tudorovo, Moldova.

AGE. — Meotian/Turolian.

MATERIALS. — (OGU 1780 type *H. tudorovense*) a skull, (OGU 906, 1783 & no No.) three jaws.

Hipparion verae Gabuniya, 1979
(originally *H. gromovae* Gab. 1959, preoccupied by *H. gromovae* Villalta & Crusafont, 1957)

TYPE LOCALITY. — Grebeniki, Moldova.

AGE. — Early Meotian/Late Vallesian/Early Turolian.

MATERIALS. — Grebeniki: University of Odessa Museum, Odessa (OGU 916, 917, 1012/1 & 1016 type) four skulls, (OGU 889, 897, 898, 905, 1016, 1462 & no No.) seven jaws; Department of Paleontology & Paleontological Museum, Kiev (No. 408-47 & 408-114) two jaws; Museum Ordzonikidze, Moscow (Nos. 2027, 2051, 2079 & no No.) four jaws, (No. 2061) a skull, said to be from Tchobruchi, resembles *H. verae*.
H. aff. *verae*: Beluska, Macedonia (former Yugoslavia): (PM 2660/196) skull, (PM 2743/195) jaw.

Proboscidipparion "pater" Matsumoto, 1927

TYPE LOCALITY. — unknown.

AGE. — Ruscinian-Villafranchian.

MATERIALS. — Nihetsun, Yushe, China: (IVPP THP 20763) skull, (IVPP THP 30756) jaw. — Loc. 26, Peihaitsun, Yushe, China (IVPP THP 14312 lectotype) skull and jaw.

Proboscidipparion rocinantis
(Hernandez-Pacheco, 1921)

TYPE LOCALITY. — Puebla de Almoradier, Spain.

AGE. — Villafranchian.

MATERIALS. — Villaroya, Spain: (IPS 2085) a skull, (IPS V 196, unreadable No. & no No.) three jaws. — Kvabebi, Georgia: Inst. Paleobiol., Tbilisi (K-48) a skull. — Shamar, Mongolia: (PIN 970/2086) a jaw. — Peihaitsun, Matsekou, Yushe, Shanxi, China: Institute of Vertebrate Paleontology & Paleoanthropology, Beijing (IVPP THP 10331 & 10508) skull, skull and jaw, (IVPP THP 10097) a jaw. — Yinkiangtsun, Yushe, China (IVPP THP 10733) skull and jaw. — Hsi Chwang/Hsiao Chuang, Shanxi, China (AMNH 96-B 1031) skull and jaw, (AMNH 64-B 815) skull.

Proboscidipparion sinense Sefve, 1927

TYPE LOCALITY. — Mien Chih Hsien, Lankou, Henan, China.

AGE. — Villafranchian.

MATERIALS. — Mien Chih Hsien: Paleontological Institute, Univ. Uppsala (M 3925 & 3926 type) skull and jaw. — Yushe, Shanxi, China: Beijing Natural History Museum (no No.) skull and jaw.

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Mise en page
Noémie de la Selle
Packaging Éditorial

Achevé d'imprimer
sur les presses de l'Imprimerie Durand
28600 Luisant (France)
Dépôt légal n° 11149

Printed on acid-free paper
Imprimé sur papier non acide

Date de distribution du fascicule 1, 1999 : 31 mars 1999

Couverture : Alternances marnes-calcaires du Lias du Bassin Lombard (Alpes Méridionales)
Coupe des gorges de la Breggia (Suisse)
Photographie J. F. Deconinck (Université de Lille I)

geodiversitas 1999 • 21 (2)

Indexed in
GeoRef (Online Database for Bibliography and Index of Geology), Biological Abstracts, ASFA (Aquatic Sciences and Fisheries Abstract), Pascal, Zoological Record

Conception Graphique : Isabel Gautray

Publication trimestrielle, juin 1999. ISSN : 1280-9659

Vente en France
Muséum national d'Histoire naturelle
Diffusion Delphine Henry
57 rue Cuvier, 75005 Paris,
France
Tél. : 33 - 01 40 79 37 00
Fax : 33 - 01 40 79 38 40
e-mail : dhenry@mnhn.fr

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